PROC. BIOL. SOC. WASH.
102(1), 1989, pp. 176–248

SPRINGSNAILS (GASTROPODA: HYDROBIIDAE) OF OWENS AND AMARGOSA RIVER (EXCLUSIVE OF ASH MEADOWS) DRAINAGES, DEATH VALLEY SYSTEM, CALIFORNIA-NEVADA

Robert Hershler

Abstract.—Thirteen springsnail species (9 new) belonging to *Pyrgulopsis* Call & Pilsbry, 1886, and *Tryonia* Stimpson, 1865 are recorded from the region encompassing pluvial Owens and Amargosa River (exclusive of Ash Meadows) drainages in southeastern California and southwestern Nevada. Discriminant analyses utilizing shell morphometric data confirmed distinctiveness of the nine new species described herein, as: *Pyrgulopsis aardahli, P. amargosae, P. owenensis, P. pertubata, P. wongi, Tyronia margae, T. robusta, T. rowlandsi,* and *T. salina.* Of the 22 springsnails known from Death Valley System, 17 have very localized distributions, with endemic fauna concentrated in Owens Valley, Death Valley, and Ash Meadows. A preliminary analysis showed only partial correlation between modern springsnail zoogeography and configuration of inter-connected Pleistocene lakes comprising the Death Valley System.

This constitutes the second part of a systematic treatment of springsnails from the Death Valley System, a large desert region in southeastern California and southwestern Nevada integrated by a series of lakes during Pleistocene times. An earlier paper (Hershler & Sada 1987) dealt with the Ash Meadows faunule, while this document provides descriptions of fauna collected during 1985–1987 survey of much of remaining portions of the System, including waters in Mono, Adobe, Long, Owens, Indian Wells, Panamint, and Death Valleys; Amargosa River drainage; and some areas adjacent to the above (Fig. 1). A brief discussion of springsnail zoogeography also is provided, although a more extensive treatment will be given following survey of remaining portions of Death Valley System (notably Mojave River drainage) and additional peripheral areas.

List of Recognized Taxa

Pyrgulopsis aardahli, new species.
P. amargosae, new species.
P. micrococcus (Pilsbry, 1893).
P. owensensis, new species.
P. perturbata, new species.
P. cf. *stearnsiana* (Pilsbry, 1899).
P. wongi, new species.
Tryonia margae, new species.
T. protea (Gould, 1855).
T. robusta, new species.
T. rowlandsi, new species.
T. salina, new species.
T. variegata Hershler & Sada, 1987.

Materials and Methods

Localities visited, consisting of low- to mid-elevation (<2500 m) springs and perennial streams, are shown in Figs. 2–7 and listed in the Appendix. Snails were found

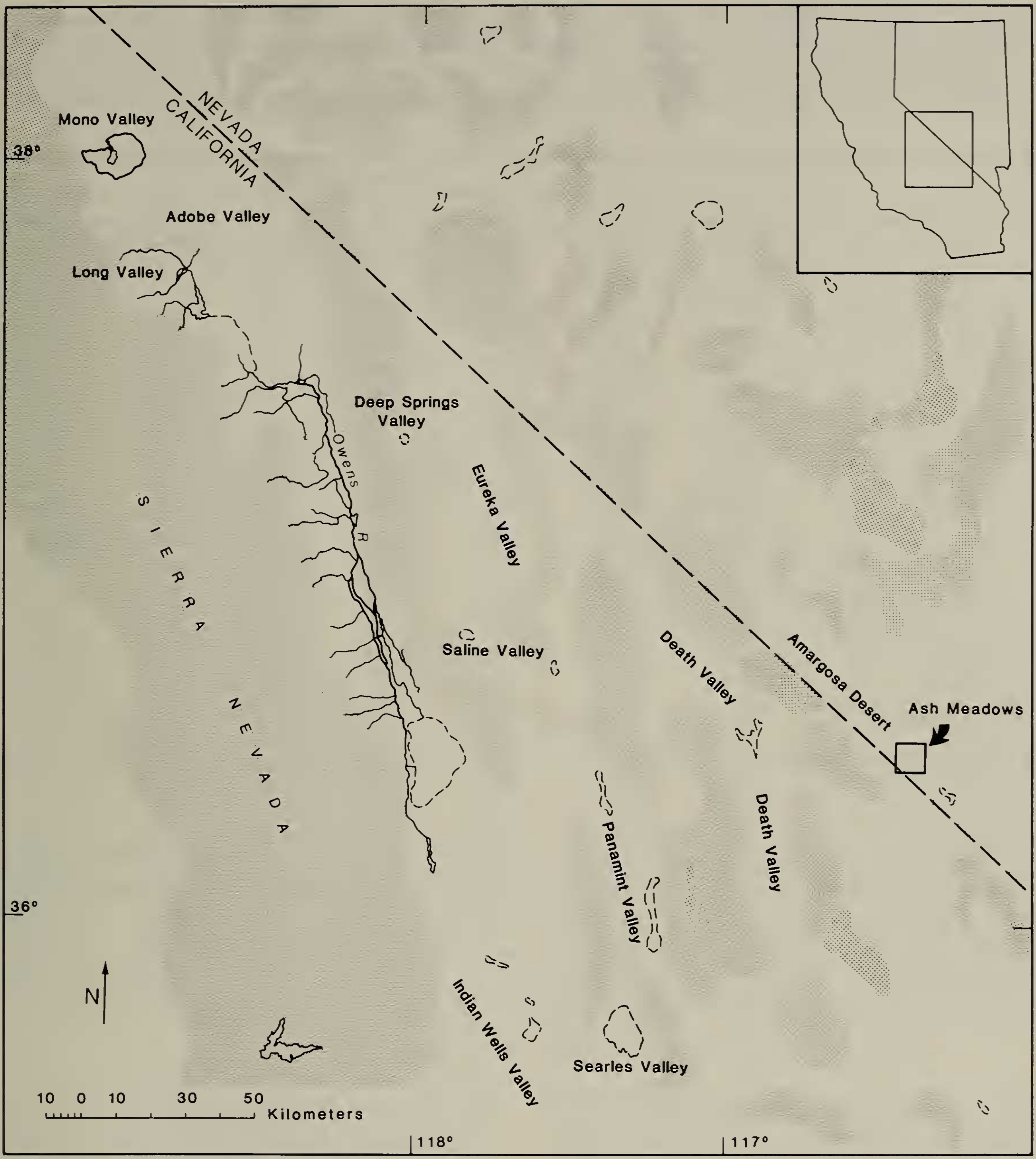

Fig. 1. Map showing desert basins of southeastern California and southwestern Nevada comprising study area. Stippled areas indicate mountain ranges.

in springs of varying sizes and appearance as well as low- to moderate-energy (spring-fed) streams. Photographs of representative sites are in Figs. 8 and 9.

Snails were relaxed in the field with menthol crystals, fixed in 4% buffered formalin and preserved in 70% ETOH. Material was collected by author unless otherwise indicated. Water temperature and conductivity were measured with a temperature-compensated, HACH 16300 conductivity meter.

Methods of anatomical study and photography of shells and other morphologic features are routine (Hershler & Sada 1987). Generalized radular formulae are based on

Table 1.—Selected shell parameters for *Pyrgulopsis* species. Shell height (SH) and width (SW) are given in mm. Data for each population include mean values (upper line) and standard deviations (lower). Number of populations and specimens for which data were obtained are given in parentheses. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = aperture shape, W = whorl expansion rate.

	Parameter						
Species	NW	SH	SW	T	D	AS	W
P. aardahli	3.98	2.90	2.20	4.24	0.56	1.15	2.11
(1, 15)	0.15	0.21	0.20	0.54	0.04	0.04	0.19
P. amargosae	3.86	1.97	1.45	4.43	0.57	1.14	2.03
(3, 45)	0.20	0.28	0.25	0.67	0.05	0.06	0.21
P. crystalis	3.17	2.02	1.95	3.44	0.50	1.18	2.56
(1, 3)	0.29	0.24	0.18	0.32	0.05	0.06	0.76
P. erythropoma	3.46	2.00	1.82	3.52	0.56	1.15	2.75
(5, 68)	0.27	0.31	0.24	0.64	0.05	0.06	0.87
P. fairbanksensis	3.29	2.67	2.23	4.23	0.61	1.09	2.80
(1, 14)	0.34	0.21	0.15	1.03	0.09	0.13	0.07
P. isolata	4.00	2.75	2.18	3.81	0.58	1.12	2.09
(1, 13)	0.14	0.13	0.11	0.36	0.03	0.04	0.20
P. micrococcus	4.16	2.16	1.42	5.17	0.62	1.19	1.89
(27, 362)	0.33	0.31	0.17	1.05	0.06	0.08	0.28
P. nanus	3.55	1.74	1.53	3.52	0.55	1.09	2.44
(3, 42)	0.24	1.74	1.53	3.52	0.55	1.09	0.34
P. owensensis	3.61	2.16	1.62	4.56	0.59	1.16	2.08
(6, 86)	0.26	0.28	0.18	0.98	0.05	0.05	0.24
P. perturbata	4.37	3.29	2.22	5.26	0.62	1.18	2.01
(3, 39)	0.19	0.39	0.31	0.85	0.62	1.18	0.19
P. pisteri	3.97	2.31	1.99	3.46	0.54	1.10	2.37
(2, 31)	0.27	0.18	0.13	0.45	0.04	0.04	0.31
P. cf. *stearnsiana*	4.14	2.52	1.68	5.73	0.61	1.24	1.97
(2, 25)	0.15	0.18	0.12	1.21	0.05	0.06	0.21
P. wongi	3.86	2.11	1.62	4.10	0.59	1.19	2.23
(19, 286)	0.27	0.39	0.24	0.70	0.05	0.05	0.29

examination of SEM micrographs from varying numbers of populations, and are presented in following order of tooth types: centrals, laterals, inner marginals, outer marginals.

Whorl counts, standard measurements, and Raupian parameters were obtained from selected series of live-collected, adult specimens, recognizable by their complete and thickened inner shell lips. After whorls were counted (NW), shells were imbedded in clay with aperture facing up and coiling axis perpendicular to the observer's line of sight. Shell outlines were traced using camera lucida (25× or 50×) and points on these digitized for calculation of the following parameters (largely following Kohn & Riggs 1975): shell height (SH), shell width (SW), length of body whorl (LBW), width of body whorl (WBW), aperture length (AL), aperture width (AW), translation rate (T), whorl expansion rate (W), distance of generating curve from coiling axis (D), and aperture shape (SA). In order to facilitate comparisons, these parameters were also obtained from the entire set of shells of Ash Meadows springsnails used in an earlier morphometric study (which involved generation of a subset of the above parameters using a somewhat different methodology; Hershler

Table 2.—Selected shell parameters for *Tryonia* species. Shell height (SH) and width (SW) are given in mm. Data for each population include mean values (upper line) and standard deviations (lower). Number of populations and specimens for which data were obtained are given in parentheses. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = aperture shape, W = whorl expansion rate.

Species	Parameter						
	NW	SH	SW	T	D	AS	W
T. angulata	5.70	3.24	1.56	7.99	0.58	1.50	1.66
(3, 39)	0.52	0.37	0.19	1.29	0.07	0.08	0.22
T. elata	5.99	1.96	0.82	8.96	0.59	1.34	1.42
(2, 30)	0.53	0.29	0.07	1.15	0.05	0.08	0.11
T. ericae	4.71	1.40	0.76	6.42	0.57	1.25	1.65
(2, 19)	0.66	0.19	0.06	1.06	0.06	0.06	0.11
T. margae	6.21	2.78	0.98	10.80	0.59	1.48	1.37
(1, 6)	0.10	0.12	0.02	0.93	0.59	0.03	0.19
T. protea	5.33	3.53	1.59	9.45	0.66	1.38	1.51
(1, 6)	0.52	0.45	0.13	0.86	0.04	0.05	0.19
T. robusta	4.22	1.63	1.06	5.03	0.60	1.25	1.81
(2, 28)	0.34	0.31	0.18	0.83	0.04	0.04	0.17
T. rowlandsi	4.34	1.95	1.19	6.21	0.62	1.21	1.69
(1, 16)	0.18	0.16	0.07	1.05	0.06	0.08	0.15
T. salina	4.83	2.89	1.70	5.72	0.53	1.25	1.64
(1, 15)	0.20	0.14	0.08	0.60	0.04	0.03	0.09
T. variegata	6.81	4.27	1.69	8.93	0.56	1.50	1.44
(17, 226)	0.91	1.18	0.32	2.02	0.07	0.11	0.15

& Sada 1987). Digitizing was done using CONCH (methodology described in Chapman et al., in prep) and a GTCO Micro-Digi Pad 12 × 12 linked to a KAYPRO 2000 microcomputer.

Descriptive statistics for all morphological variables were obtained for each population and species, and a selection of these are summarized (by species) in Tables 1 and 2. Discriminant analysis (DA) incorporated all of the shell morphometric parameters and were constructed using all specimens measured for each species (considered as separate groups). All computations were performed using SYSTAT (Wilkinson 1986) on an IBM-AT.

Systematics

Generic diagnoses are in Hershler & Sada (1987). Species accounts include common name, synonomy, material examined (localities numbered [in parentheses] as in Appendix), diagnosis, description, remarks, type locality, distribution and habitat, etymology, and remarks. Asterisked (*) lots were used for shell measurements. Descriptions emphasize distinctive features from shell, radula, body pigmentation, and reproductive systems of both sexes.

Family Hydrobiidae Troschel, 1857

Genus *Pyrgulopsis* Call & Pilsbry, 1886

Pyrgulopsis aardahli, new species

Benton Valley springsnail

Figs. 10–14

Material examined.—California: Mono Co.; Spring at Bramlette Ranch (87), USNM 860406 (holotype), *857951 (paratypes), 21 Apr 1987.

Diagnosis.—A large-sized species with broadly conical shell. Penis with elongate filament, very small lobe, and ventral swelling. Penial glandular ridges, 1–3.

Description.—Shell (Fig. 10) 2.6–3.4 mm

Fig. 2. Sampling localities in southern Owens Valley and western Indian Wells Valley. Solid lines indicate selected elevation contours (light) and modern drainage (dark; stipple indicates lakes); dashed lines indicate historic drainage, including dry lake beds.

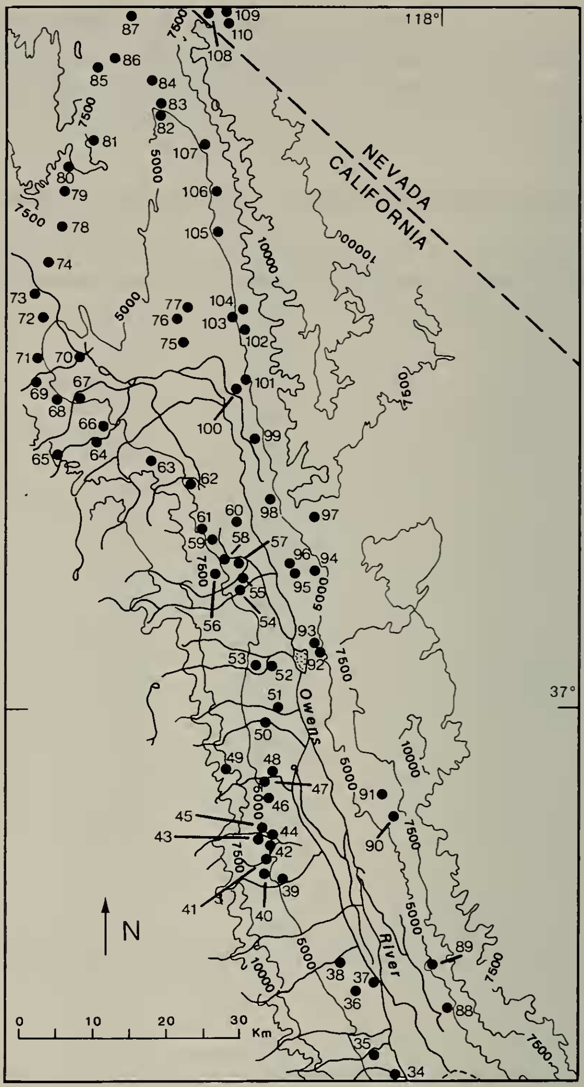

Fig. 3. Sampling localities in northern Owens Valley.

high, height/width, 140–170%. Whorls, 3.75–4.25, moderately convex, moderately shouldered. Body whorl inflated, height 76–82% of that of shell. Aperture ovate, apertural plane near-parallel to coiling axis (Fig. 10c). Inner lip thickened, slightly reflected, adnate to small portion of or slightly separated from body whorl. Outer lip straight, thin. Umbilicus moderately open.

Dark, grey-black epithelial (melanic) pigment on most of snout (to just posterior of cephalic tentacles), along anterior edge of foot, on operculigerous lobe (Fig. 11). Central portions of sides of head/foot lightly dusted or unpigmented. Tentacles unpigmented except for dark ring along bases. Brown-black subepithelial pigment granules sometimes forming dark band along posterior edge of "neck."

Radular (Fig. 12) formula: 5–1–5/1–1, 2(3)–1–3, 22–24, 28–32 (from paratypes). Central tooth broadly trapezoidal; basal process moderately excavated. Penis (Fig. 13b–e) large (extending beyond mantle collar), thin, considerably longer than wide. Filament slender, moderate in length. Lobe reduced or absent, with blunt distal edge. Large, elongate glandular ridge borne on elongate swelling of ventral penial surface. Single, smaller ridges sometimes found on

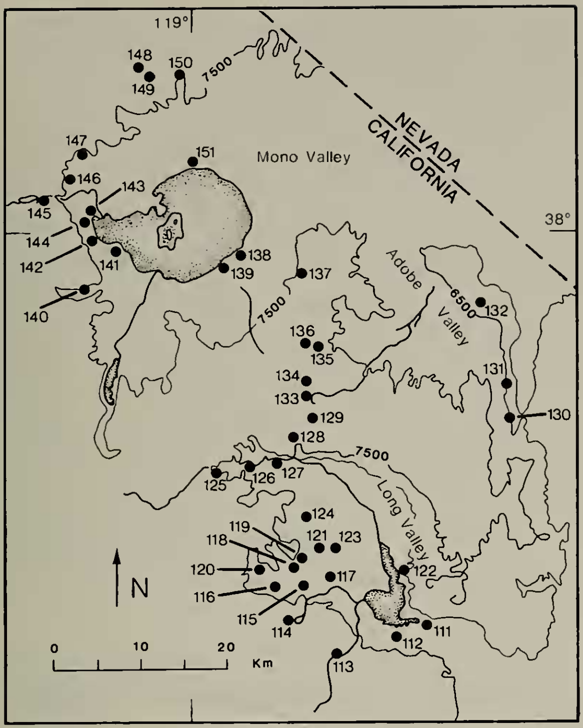

Fig. 4. Sampling localities in Mono, Long, and Adobe Valleys.

tip of lobe, and on dorsal penial surface proximal to base of filament. Filament darkly pigmented with subepithelial granules (Fig. 13b). Capsule gland sub-equal to albumen gland (Fig. 13a). Seminal receptacle minute, positioned entirely anterior to bursa copulatrix. Bursa pear-shaped, moderate in size relative to pallial oviduct, positioned partly posterior to albumen gland.

Type locality.—Spring at Bramlette Ranch in Benton Valley, Mono County, California.

Distribution and habitat.—Endemic to type locality (Fig. 14). Common in dense watercress in uppermost portion of outflow of small, highly degraded spring (20°C, 190 micromhos/cm).

Etymology.—Named after Jeffrey B. Aardahl, Bureau of Land Management (California Desert District), who provided diverse forms of assistance throughout the tenure of this project.

Remarks.—Distinguished from similar *P. perturbata* by shell appearance and highly reduced penial lobe.

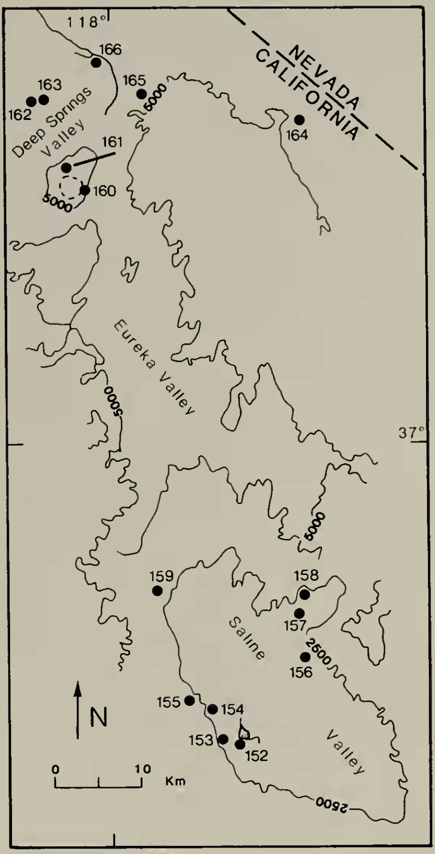

Fig. 5. Sampling localities in Saline, Eureka, and Deep Springs Valleys.

Pyrgulopsis amargosae, new species
Amargosa springsnail
Figs. 15, 16, 17a, b, 18, 19

Material Examined.—California: San Bernardino Co.; Saratoga Spring (204), USNM 860401 (holotype), *853515 (paratypes), 7 Feb 1985; 857972, 10 Jul 1986.—Inyo Co.; Spring crossing path on south side of Amargosa Gorge (208), *853516, 13 Mar 1986; 857973, 16 Mar 1987.—Spring feeding Amargosa River in Amargosa Gorge (208), 853517, 13 Mar 1985.—Spring in marsh east of Grimshaw Lake (209), *853518, 13 Mar 1985.

Diagnosis.—A small-sized species with globose to low conical shell. Penis large relative to head/foot; penial lobe reduced; filament long, wide. Penial glandular ridges, 0–2.

Description.—Shell (Fig. 15) 1.5–2.7 mm high, height/width, 110–160%. Whorls, 3.5–

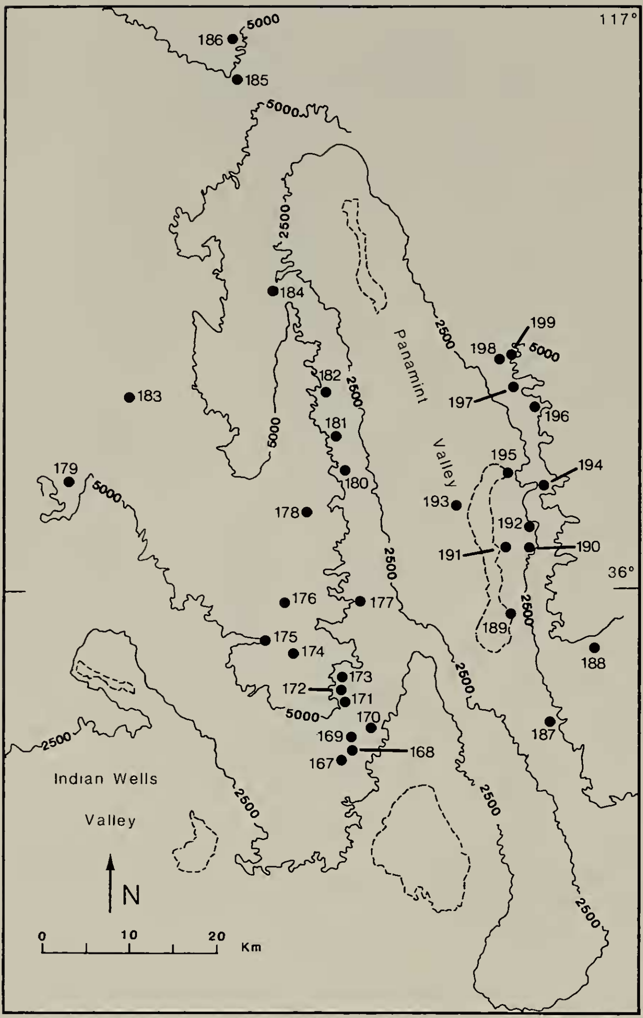

Fig. 6. Sampling localities in Panamint and northern Indian Wells Valleys.

4.25, convex, moderately shouldered. Body whorl 74–85% of shell height. Apex, parts of teleoconch whorls often appearing white due to erosion. Aperture broadly ovate, apertural plane near-parallel to coiling axis (Fig. 15b). Inner lip thickened, reflected above, adnate to small portion of or slightly separated from body whorl. Outer lip straight, thin. Umbilicus chink-like to broadly open. Spiral striations sometimes prominent on teleoconch.

Dark, brown-black epithelial pigment on most of snout (except distal tip), along anterior and posterior edges of "neck" (central area lighter), on part or all of operculigerous lobe. Tentacles lightly pigmented.

Radular (Fig. 16) formula: 5(6)–1–5(6)/1-1, 3–1–4, 27–28, 24–26 (from paratypes). Central tooth broadly trapezoidal; basal process moderately excavated. Penis (Figs. 17a, b, 18b–e) thickened, longer than wide. Filament much longer than lobe, about equal to remaining penis length. Lobe narrow, variable in shape (Fig. 18b–e). Filament having highly muscular appearance; surface lined with weak striations. One or two small glandular ridges sometimes present at tip of lobe. Dark, grey-black subepithelial pigment filling filament length almost to distal tip as well as portions of remaining distal penis (Fig. 18b). Albumen and capsule glands about equal in length (Fig. 18a). Seminal receptacle minute, positioned well anterior to bursa copulatrix. Bursa copulatrix club-shaped, small, positioned partly posterior to albumen gland.

Type locality.—Saratoga Spring, southern Death Valley, San Bernardino Co., California.

Distribution and habitat.—Found in a few near-brackish springs along lower course of Amargosa River at Saratoga Spring, Amargosa Gorge, and Grimshaw Lake area (Fig. 19). Type locality an extensive marsh area (with several large, open pools) fed by several small springs. Snails were common in westernmost spring, both on rocks and submergent macrophytes in small springpool (28°C, 5000 micromhos/cm), and on emergent sedges and firm bottom in shallow stream outflow. At other localities, consisting of small rheocrenes (16–27°C, 2000-10, 150 micromhos/cm), snails were common on all substrates.

Etymology.—Referring to distribution along Amargosa River.

Remarks.—Distinguished from *P. micrococcus* by globose shell; large penis; large penial filament; small, narrow penial lobe; and highly reduced glandular ridge. Ranges of these very similar snails (previously confused by Hershler and Sada 1987:788) are contiguous.

Pyrgulopsis micrococcus (Pilsbry, 1893)
Oasis Valley springsnail
Figs. 17c, d, 20–25

Amnicola micrococcus Pilsbry in Stearns, 1893:277.

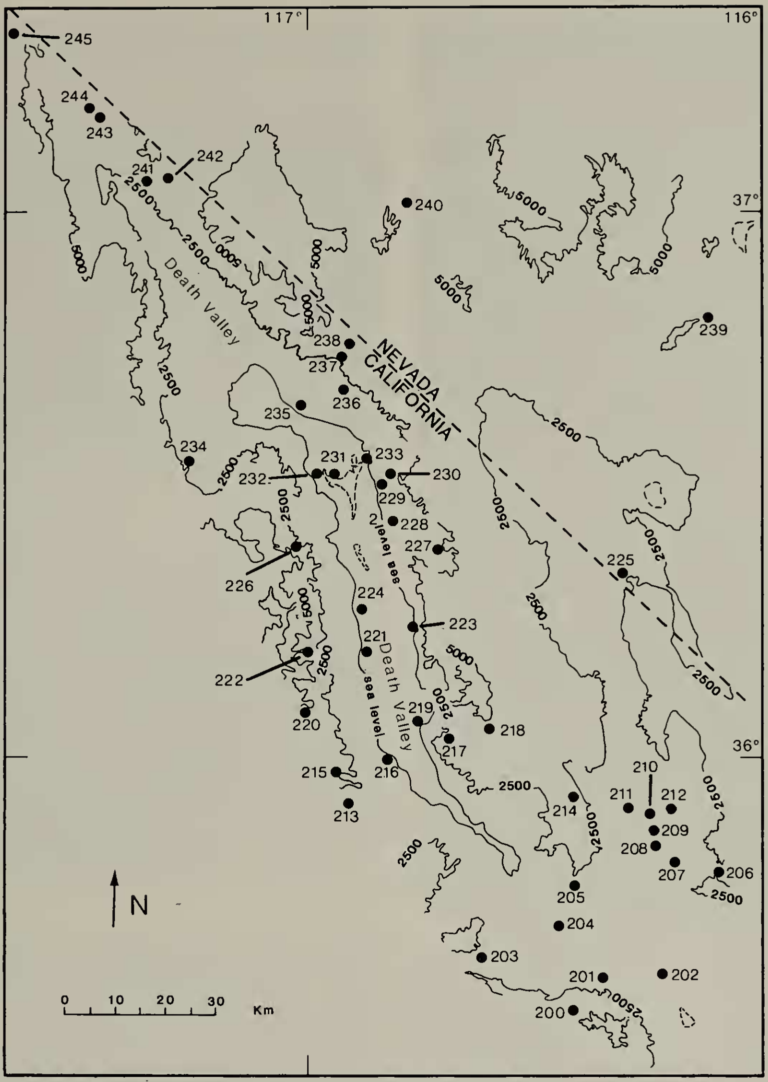

Fig. 7. Sampling localities in Death Valley and Amargosa Basin.

Material examined.—Nevada: Nye Co.; Spring in Oasis Valley (204), USNM *850297, 18 Nov 1985; 857961, 16 Mar 1987.—Cane Spring (239), *857936, 10 July 1986.—California: Inyo Co.; Northernmost of Tecopa Hot Springs (210), *853502, 12–13 Mar 1985; 857962, 16 Mar 1987.—Shoshone Spring (211), *853501, 12 Mar 1985; 857962, 16 Mar 1987.—Grapevine Springs (241): northwest-most spring in complex, 853503, 1 Mar 1985; Spring emerging below limestone bench northwest of ranch, 853504, 26 Feb 1985; Spring on bench above ranch, 853505, 25 Feb 1985; Spring at ranch, *853506, 25 Feb 1985; 857964, 14 Mar 1985.—Spring 1.6 km east of Scotty's Castle (242), *853507, 26 Feb 1985; 857965, 14 Mar 1987.—Hanaupah Spring (222), *853508, 16 Feb 1985; 857966, 21 Mar 1987.—Lower spring in Johnson Canyon (220), *853509, 18 Feb 1985; 857967, 21 Mar 1987.—Stream in Jail Canyon (196), *853513, 14 Feb 1985; 857970, 19 Mar 1987.—Stream in Surprise Canyon (194), *857937, 19 Mar 1987; Stream in Pleasant Canyon (190), *857940, 19 Mar 1987.—China Garden Spring (184), 853511, 9 Feb 1985.—Stream below Darwin Falls (184), 857969, 23 Mar 1987.—Spring above Darwin Falls (184), *853512, 10 Feb 1985.—Stream in Snow Canyon (182), *857938, 16 Sep 1987, J. Aardahl!—Stream in Knight Canyon (180), *857939, 14 Apr 1987.—Tennessee Spring (178), *853514, 4 Mar 1985; 857971, 13 May 1987.—Saline Marsh (152), *853510, 10 Feb 1985; 857968, 28 Mar 1987.

Diagnosis.—A small-sized species, with

Fig. 8. Photographs of selected springsnail localities: a, stream in Cottonball Marsh, Death Valley, type locality of *T. salina* (3-10-87; photo by P. Rowlands); b, Grapevine Springs, Death Valley, type locality of *T. margae* and *T. rowlandsi* is on the large travertine mound (3-14-87); c, Saline Marsh, Saline Valley (3-29-87); d, Sand Canyon stream, Indian Wells Valley (3-26-87); e, Fish Slough, Owens Valley, spring sources (including type locality of *P. perturbata*) visible in lower portion of photograph (ca. 1975; aerial photo by P. Pister); f, "NE" Spring at Fish Slough (2-7-85).

globose to ovate-conic shell. Penis with moderate-sized lobe; distal edge of lobe usually ornamented with glandular ridge.

Description.—Shell (Figs. 20, 21) 1.1–3.1 mm high, height/width, 99–190%. Whorls, 3.25–5.0, well-rounded, with slight shoulders. Spire often irregularly convex due to bulging of whorls. Body whorl 65-89% of shell height. Aperture ovate, apertural plane near-parallel to coiling axis (Fig. 21b). Inner lip moderately thickened and reflected, usually slightly separated from body whorl. Outer lip straight, thin. Umbilicus chink-like to moderately open.

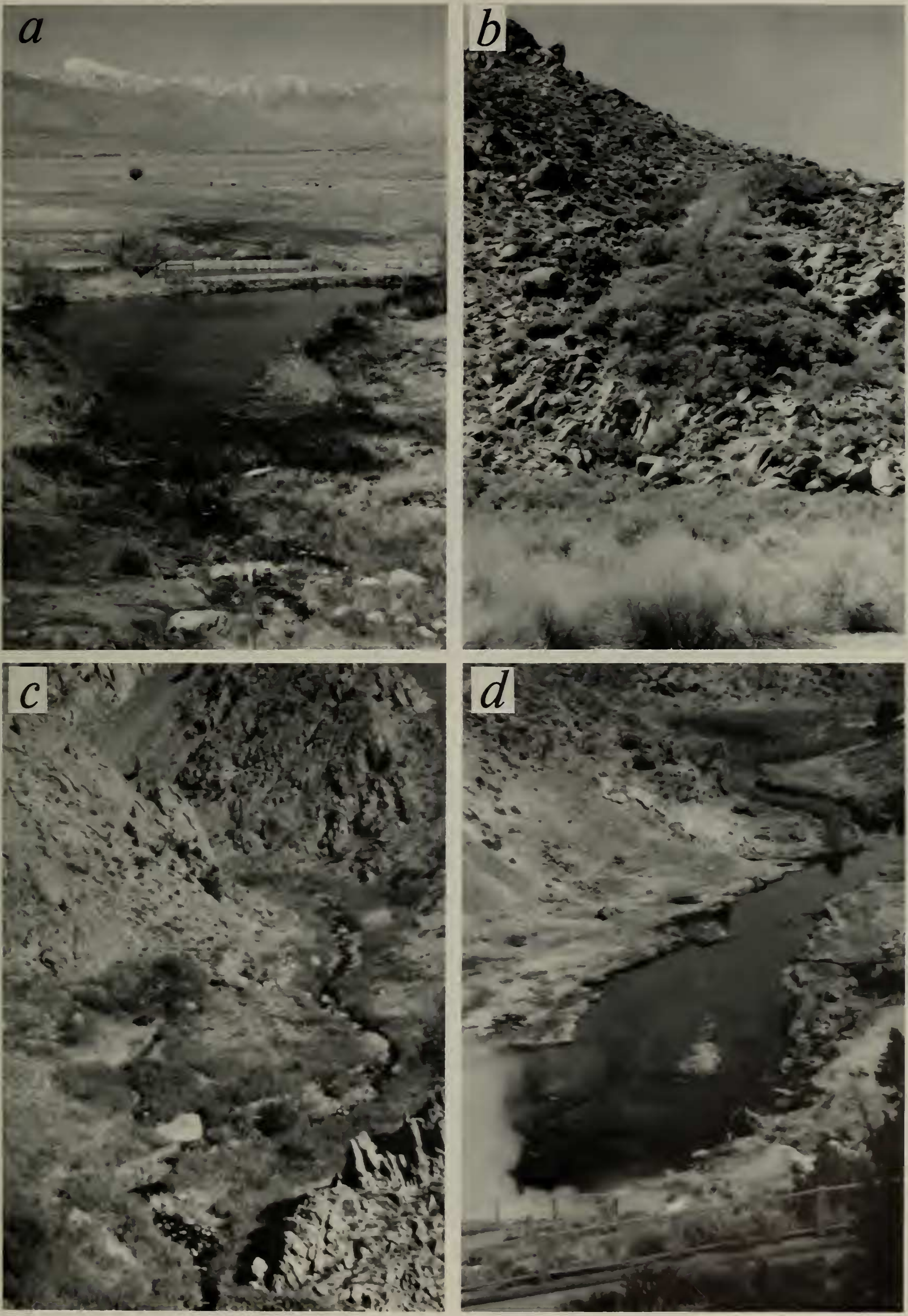

Fig. 9. Photographs of springsnail localities: a, Warm Springs, Owens Valley (4-19-87); b, Small spring S of Warren Lake, Owens Valley (4-18-87); c, Spring in Owens Gorge, Owens Valley (5-7-87); d, Hot Creek, Long Valley (4-23-87).

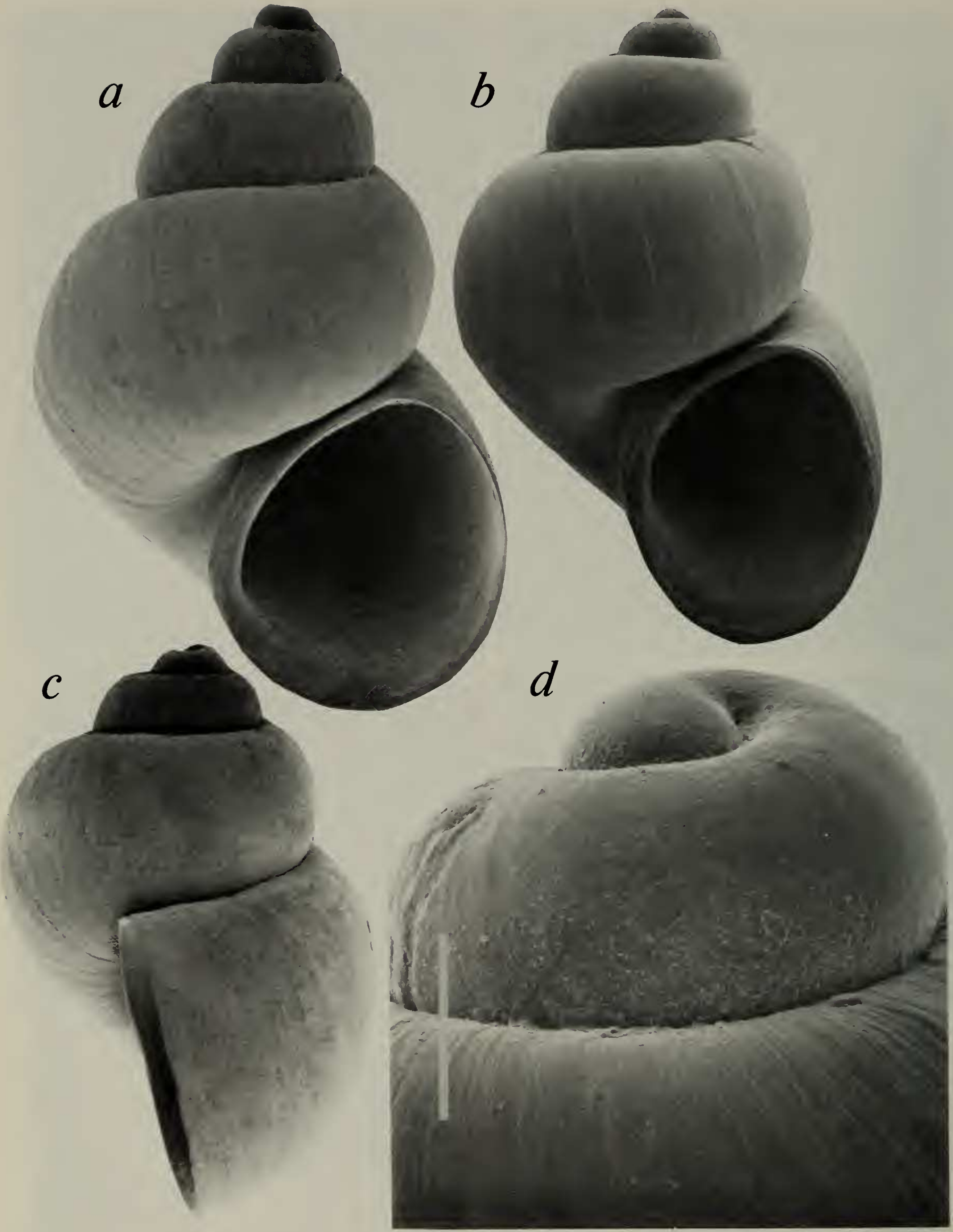

Fig. 10. SEM micrographs of *P. aardahli* from spring at Bramlette Ranch: a, Holotype, USNM 860406 (shell height, 3.26 mm); b–d, Paratypes, USNM 857951 (scale of "b" and "c" as in "a"; bar = 150 μm).

Head/foot epithelial pigment ranging from absent to near-uniformly black (lighter on central portions of sides of "neck").

Radular (Figs. 22, 23) formula: (4–7)–1–(4–7)/1–1, (2–4)–1–(3–6), 17–26, 19–32 (from numerous populations). Central tooth moderately to broadly trapezoidal; basal process moderately excavated.

Penis (Figs. 17c, d, 24b–i) barely extending beyond mantle collar, moderately thickened, longer than wide. Filament slender, usually extending well beyond edge of lobe. Lobe highly variable in size and shape, tapering slightly distally. Glandular ridge (rarely absent) small, positioned on or near distal edge of lobe. Capsule gland smaller than albumen gland (Fig. 24a). Seminal receptacle small, positioned largely anterior to bursa copulatrix. Bursa pear-shaped, small to fairly large relative to pallial oviduct, most of length positioned on albumen gland.

Type locality.—Small spring in Oasis Valley, Nye County, Nevada (precise location unknown).

Distribution and habitat.—A widespread form (contrary to Taylor 1985:317) found in small springs and stream outflows (see Figs. 8b, c) of Amargosa River drainage as well as interior drainage in Death, Panamint, and Saline Valleys (5–32°C, 300–4000 micromhos/cm) (Fig. 25). Typically common on stone, bits of travertine, watercress, and plant debris.

Pyrgulopsis owensensis, new species
Owens Valley springsnail
Figs. 26a–d, 27–32

Material examined.—California: Inyo Co.; Spring ca. 1.6 km south of Mule Spring (92), USNM 853541, 5 Dec 1987, D. Giuliani.—Mule Spring (93), *853540, 19 Nov 1985, D. Wong; 857983, 20 Apr 1987.—Spring at Graham Ranch (94), *853543, 8 Feb 1985; 857985, 19 Apr 1987.—Wilkerson Springs (96), *853542, 8 Feb 1985; 857984, 18 Apr 1987.—Spring at Toll House (97), *857950, 26 Apr 1987.—Warm Springs (98), Main spring, *853544, 7 Feb 1985, 857988, 19 Apr 1987; Small spring north of above, 853545, 7 Feb 1985; 857989, 19 Apr 1987. Mono Co.: Stream in canyon S of Piute Creek (104), 860404 (holotype), *857955 (paratypes), 8 May 1987.—Springs on bench south of Piute Creek (103), North spring, 857986, 21 Apr 1987; South spring, 857987, 22 Apr 1987.

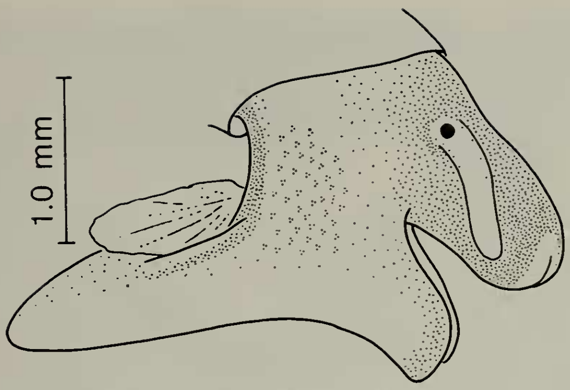

Fig. 11. Right lateral view of head-foot of *P. aardahli,* USNM 857951, spring at Bramlette Ranch. Stipples indicate pigmented areas.

Diagnosis.—A small- to moderate-sized species with globose to ovate-conic shell. Penis large relative to head/foot, filament short, lobe enlarged, ventral swelling present. Penial glandular ridges, 2–6.

Description.—Shell (Figs. 26a–d, 27, 28) 1.5–2.8 mm high, height/width, 110–160%. Whorls, 3.0–4.25, well-rounded, sutures slightly impressed. Protoconch sometimes slightly tilted. Body whorl inflated, height 74–90% of that of the shell. Apical whorls sometimes eroded, shell often covered by deposits. Aperture ovate, angled above; moderate to large in size. Aperture plane near-parallel to somewhat tilted relative to coiling axis (Figs. 27b, 28b). Inner lip slightly to considerably thickened and reflected, adnate to or (more commonly) slightly separated from body whorl. Outer lip thin, straight or slightly sinuate. Umbilicus chink-like to moderately open.

Dark brown or grey-black epithelial pigment on snout, peripheral portions of

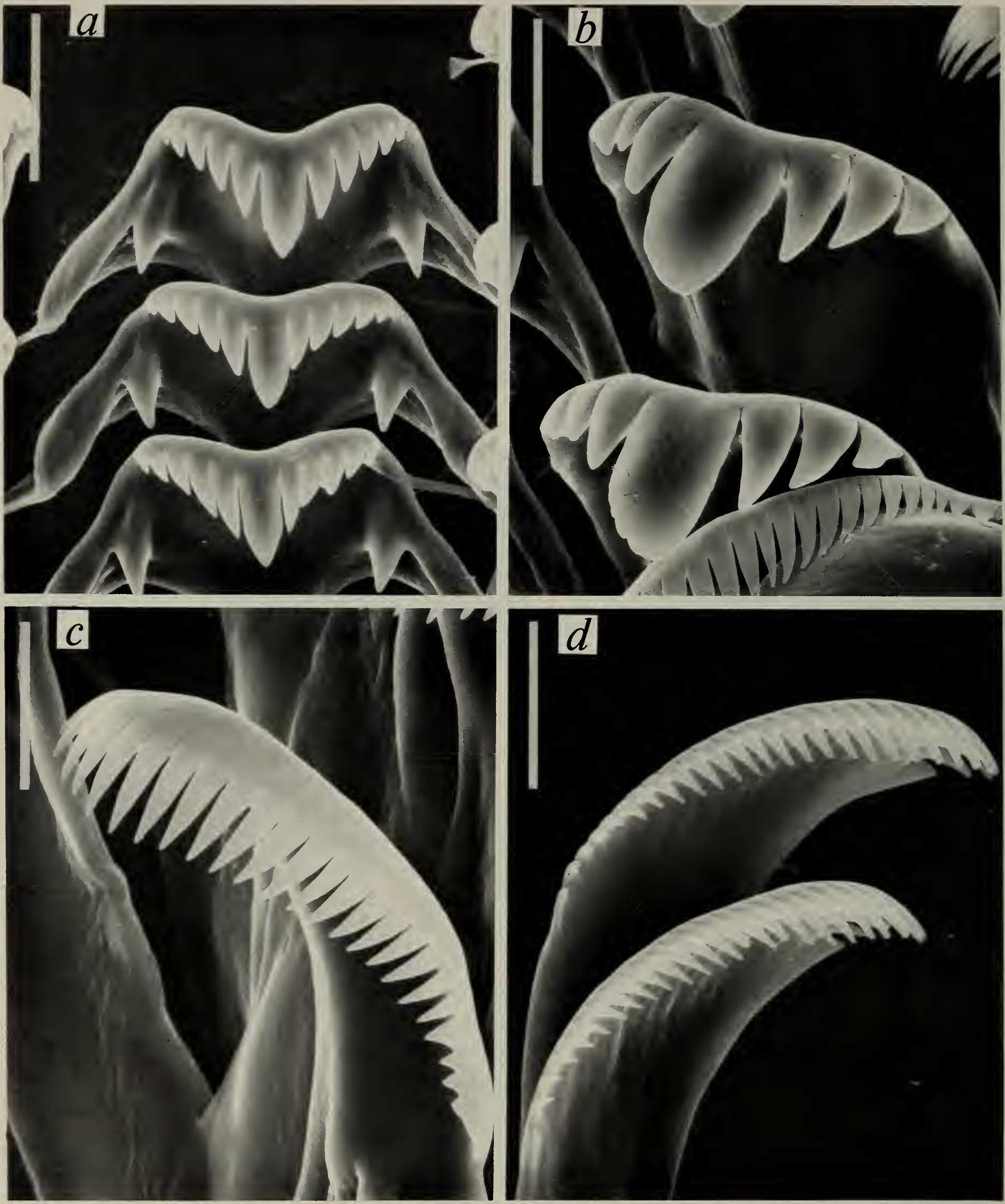

Fig. 12. Radula of *P. aardahli,* USNM 857951, spring at Bramlette Ranch: a, Centrals (bar = 12 μm); b, Laterals (bar = 8.6 μm); c, Inner marginal (bar = 6.7 μm); d, Outer marginals (bar = 6.0 μm).

"neck," and dorsal surfaces of tentacles. Dark subepithelial granules prominent in central areas of sides and sometimes along posterior edges of "neck."

Radular (Figs. 29, 30) formula: 5(6)–1–5(6)/1–1, 3–1–3(4), 18–23, 25–37 (from three populations). Central tooth broadly trapezoidal; basal process well-excavated.

Penis (Fig. 31b–i) extending well beyond mantle collar, elongate. Narrow filament shorter than lobe. Lobe massive, tapering only slightly, distal edge blunt. Edge of lobe ornamented with single elongate or two shorter glandular ridges. Dorsal penis sometimes having small glandular ridges on lobe and/or near base of filament. Ventral swelling small, located filament base. Ridge ornamenting swelling variably-sized. Filament darkly pigmented with sub-epithelial granules along most of length (Fig. 31b). Capsule gland equal to (Fig. 31a) or slightly smaller than albumen gland. Seminal receptacle minute, positioned largely or entirely anterior to bursa. Bursa pear-shaped, small- to moderate-sized, with about half of length posterior to albumen gland.

Type locality.—Stream in canyon S of Piute Creek, Mono Co., California.

Distribution and habitat.—Found along escarpments of White and Inyo Mountains east side of Owens Valley (Fig. 32). Habitat consisting of small springbrooks (10–29°C, 300–780 micromhos/cm) (Fig. 9a) where snails typically common in watercress and/or on bits of travertine and stone. Syntopic with *P. wongi* in spring at Toll House.

Etymology—Referring to occurrence in Owens Valley.

Remarks.—Distinguished from similar *P. perturbata* by shell appearance, more enlarged penial lobe, and (usually) more numerous penial glandular ridges.

Pyrgulopsis perturbata, new species
Fish Slough springsnail
Figs. 26e–g, 33–36

Material examined.—California: Mono Co.; Fish Slough: "Northwest Springs," South spring (76), USNM 860407 (holotype), *853546 (paratypes), 7 Feb 1985; 857990, 24 Apr 1987; "Northwest Springs," North spring (76), 853547, 7 Feb 1985; 857991, 20 Apr 1987; "NE Spring" (77), *853548, 7 Feb 1985; 857992, 20 Apr 1987; "BLM Spring" (75), *853549, 7 Feb 1985.

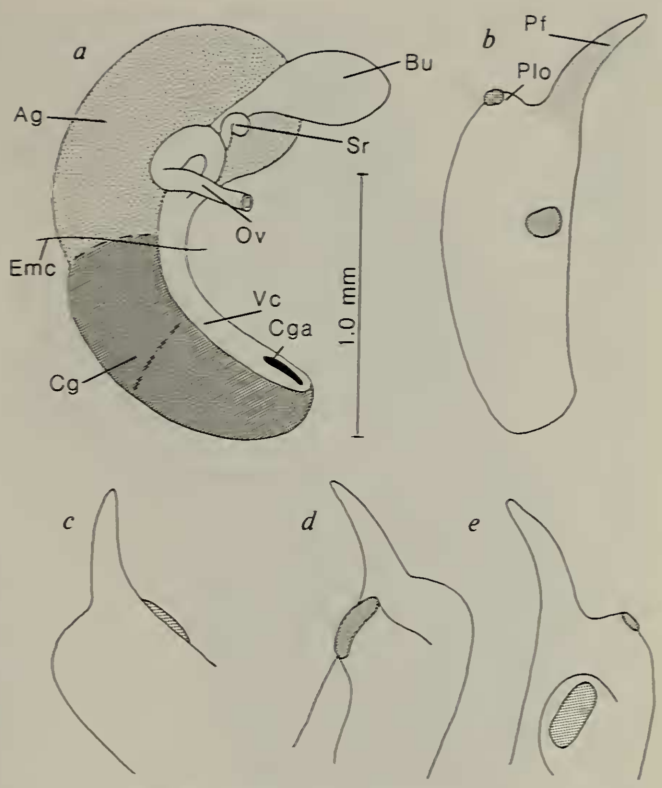

Fig. 13. Reproductive anatomy of *P. aardahli*, USNM 857951, spring at Bramlette Ranch: a, Left lateral view of pallial oviduct complex; b–e, Penes (b, c, dorsal; d, e, ventral). Stippled areas on penes indicate glandular ridges (enclosed stipples) and pigmented regions (open). Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cga = capsule gland opening; Emc = posterior end of pallial cavity; Ov = oviduct; Pf = penial filament; Plo = penial lobe; Sr = seminal receptacle; Vc = ventral channel of capsule gland.

Diagnosis.—A large-sized species with thickened, low-conical shell. Penis large, lobe and filament small, ventral swelling present. Penial glandular ridges, 3 or 4.

Description.—Shell (Figs. 26e–g, 33) 2.7–4.0 mm high, height/width, 130–180%. Whorls, 4.25–5.0, only slightly convex, with pronounced sub-sutural angulations. Body whorl inflated, 71–85% of shell height. Aperture broadly ovate. Apertural plane tilted relative to coiling axis (Fig. 33b). Inner lip usually well-thickened and reflected, broadly adnate to body whorl. Outer lip straight, thin or moderately thickened. Umbilicus chink-like.

Dark brown-black epithelial pigment prominent on snout, tentacles, and peripheral portions of sides of head/foot. Pigment

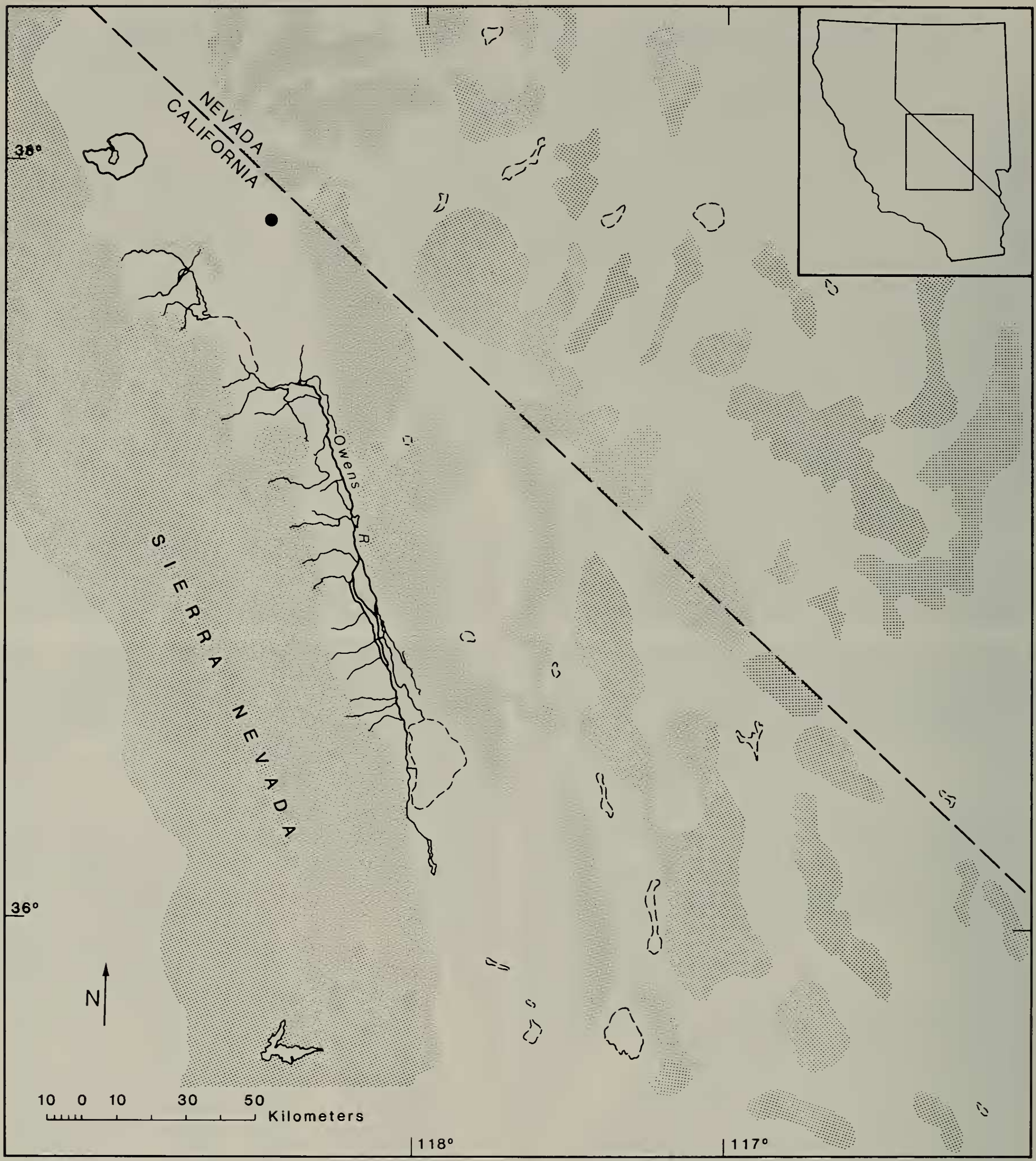

Fig. 14. Map showing distribution of *P. aardahli.*

either light or absent on central portions of sides of head/foot.

Radular (Fig. 34) formula: 5–1–5/1–1, 3–1–4(5), 18–19, 29–31 (from paratypes). Central tooth broadly trapezoidal, basal process well-excavated. Penis (Fig. 35b–e) extending well beyond edge of mantle collar, thin, considerably longer than wide. Filament both narrow and short, barely extending beyond tip of lobe. Lobe tapering only slightly distally, bearing elongate glandular ridge along distal edge. Dorsal surface of penis with small ridge proximal to base of filament. Ventral swelling arising slightly

Fig. 15. SEM micrographs of *P. amargosae* from Saratoga Spring: a, Holotype, USNM 860401 (2.28 mm); b, c (bar = 136 μm), Paratypes, USNM 853515.

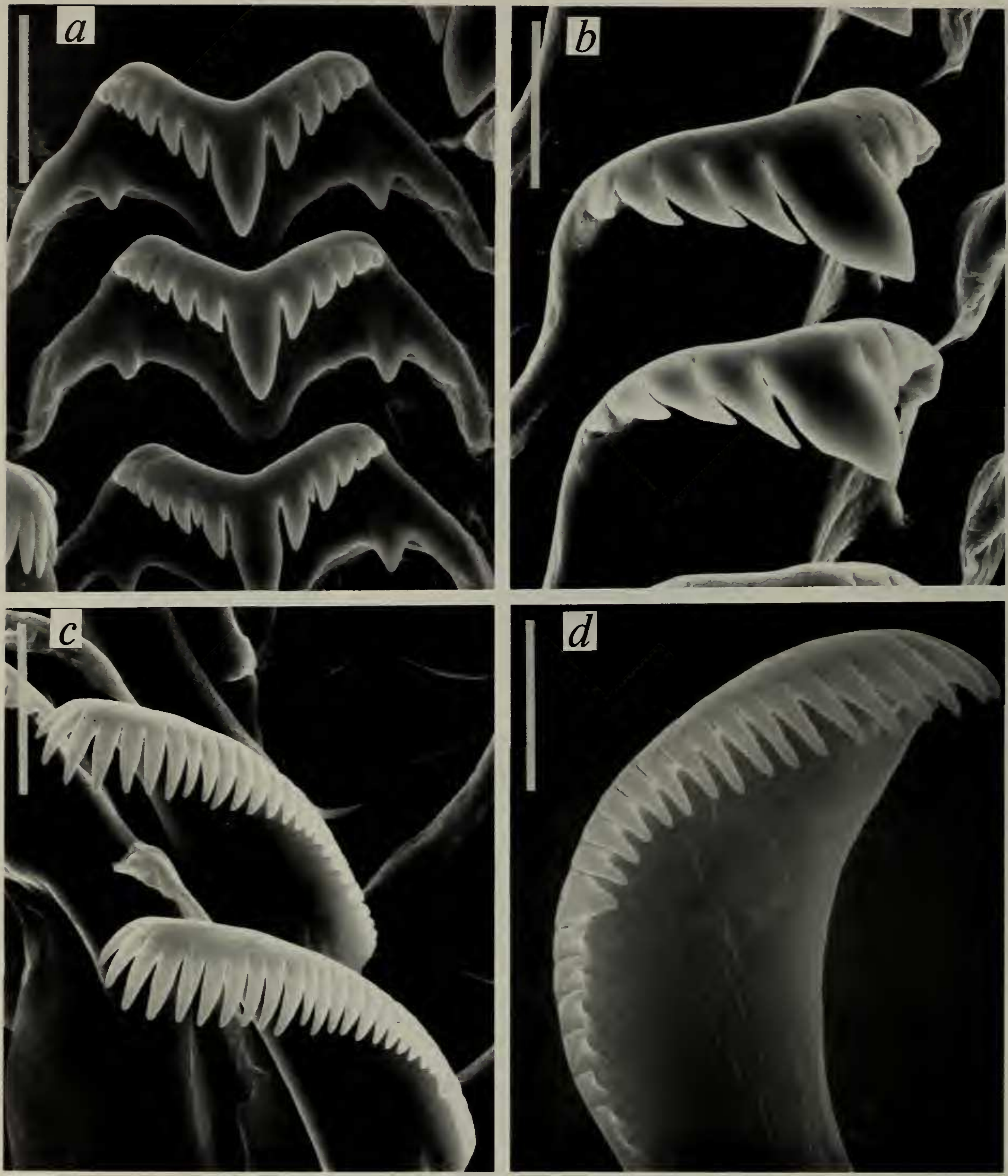

Fig. 16. Radula of *P. amargosae,* USNM 853515, Saratoga Spring: a, Centrals (bar = 12 μm); b, Laterals (bar = 8.6 μm); c, Inner marginals (bar = 8.6 μm); d, Outer marginal (bar = 3.8 μm).

proximal to base of filament; ridge (rarely two) on swelling elongate. Filament darkened along much of length by sub-epithelial pigment granules. Capsule gland sub-equal to albumen gland (Fig. 35a). Bursa small, with ca. 50% of length posterior to albumen gland. Seminal receptacle minute, positioned entirely anterior to bursa.

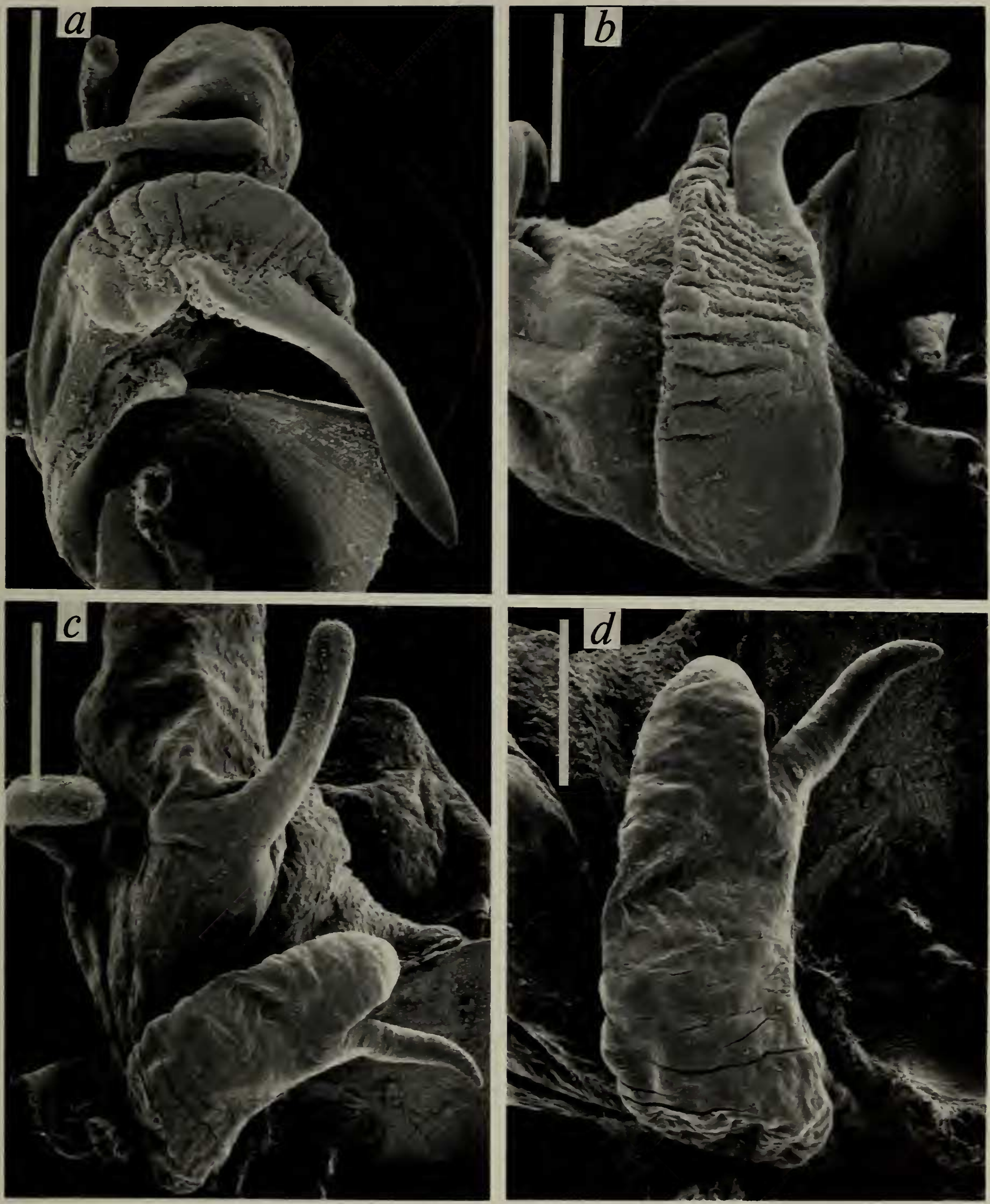

Fig. 17. SEM micrographs of head-foot and dorsal penes of *P. amargosae* and *P. micrococcus*: a (bar = 0.43 mm), b (bar = 0.38 mm), *P. amargosae*, USNM 853515, Saratoga Spring; c (bar = 0.3 mm), d (bar = 200 μm), *P. micrococcus*, USNM 857961, spring in Oasis Valley.

Type locality.—"Northwest Springs," south springpool, Fish Slough, Mono Co., California.

Distribution and habitat.—Found in three of the four main springs in Fish Slough (extinct in "BLM Spring") (Figs. 8e, f, 36). Springs issuing relatively cool (22–26°C), soft (200–360 micromhos/cm) water. Snails found only in small vestiges of rheocrene habitat at various small orifices in northwest springs (rare at both sites on vegetation and stones), and at beginning of outflow from "NE Spring" (common in *Chara*).

Etymology.—Referring to various disturbances to endemic locale, including severe reduction of original rheocrene habitat as unanticipated side effect of efforts to conserve Owens pupfish (Miller and Pister 1971).

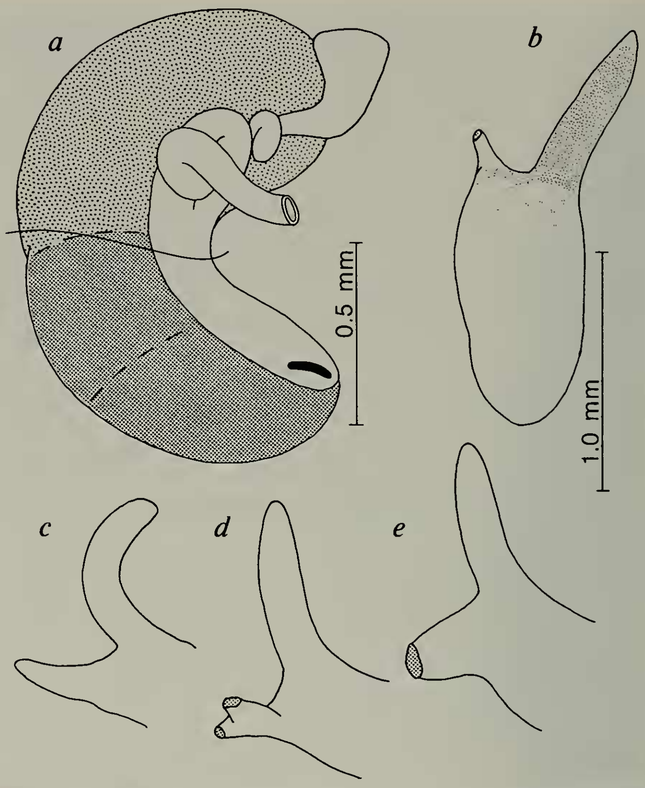

Fig. 18. Reproductive anatomy of *P. amargosae*: a, Left lateral view of pallial oviduct complex, USNM 853515, Saratoga Spring; b, c, Dorsal penes, USNM 853515, Saratoga Spring; d, e, Dorsal penes, USNM 857973, spring in Amargosa Gorge. "b" through "e" drawn to same scale.

Pyrgulopsis cf. *stearnsiana*
(Pilsbry, 1899)
Figs. 37–40

Paludestrina stearnsiana Pilsbry, 1899:124.
Fontelicella stearnsiana.—Gregg & Taylor 1965:108.
Pyrgulopsis stearnsiana.—Hershler & Thompson 1987:30.

Material examined.—California: Kern Co.; Stream in Sage Canyon (1), USNM *853520, 26 Mar 1987; 857975, 10 Nov 1987.—Stream in Sand Canyon (6), *853519, 26 Mar 1987; 857974, 22 Dec 1987, J. Aardahl.

Diagnosis.—A small-sized species with low conical shell. Penis small relative to head/foot, penial lobe reduced, filament elongate, ventral swelling present. Penial glandular ridges, 1–3.

Description.—Pertaining only to populations in study area. Shell (Fig. 37) 2.0–2.9 mm high, height/width, 130–170%. Whorls, 4.0–4.5, convex. Body whorl ca. 75% of shell height. Shell surface encrusted with thick, black deposits. Aperture broadly ovate, somewhat angled above, about half as tall as body whorl. Inner lip slightly thickened and reflected, adnate to small portion of or slightly separated from body whorl. Outer lip straight, thin; apertural plane slightly tilted relative to coiling axis (Fig. 37b).

Dark, grey-black epithelial pigment on most of snout (except distal tip), proximal portion of cephalic tentacles, along anterior and posterior edges of "neck," part or all of operculigerous lobe. Pigment on central portions of sides of neck absent to dark (subepithelial pigment cluster dense in area).

Radular (Fig. 38) formula: 5(6)–1–5(6)/1–1, 2(3,4)–1–3(4,5), 23–24, 23–29 (from single population). Central tooth broadly trapezoidal; basal process moderately excavated. Penis (Fig. 39b–e) rarely protruding beyond edge of mantle collar, longer than wide. Filament slender, sub-equal to remaining penis length. Reduced lobe scarcely

Fig. 19. Map showing distribution of *P. amargosae.*

projecting distal to base of filament. Tip of lobe often ornamented with small glandular ridge; similar, single ridges on dorsal penial surface about halfway from base of penis to base of filament, on ventral surface near (sometimes on) inner edge. The latter ridge enlarged, borne on low swelling (Fig. 39e). Filament with dark sub-epithelial pigment streak (Fig. 39b). Albumen gland sub-equal to capsule gland (Fig. 39a). Seminal receptacle small, positioned anterior to bursa copulatrix. Bursa copulatrix small relative to capsule gland, positioned partly posterior to gland.

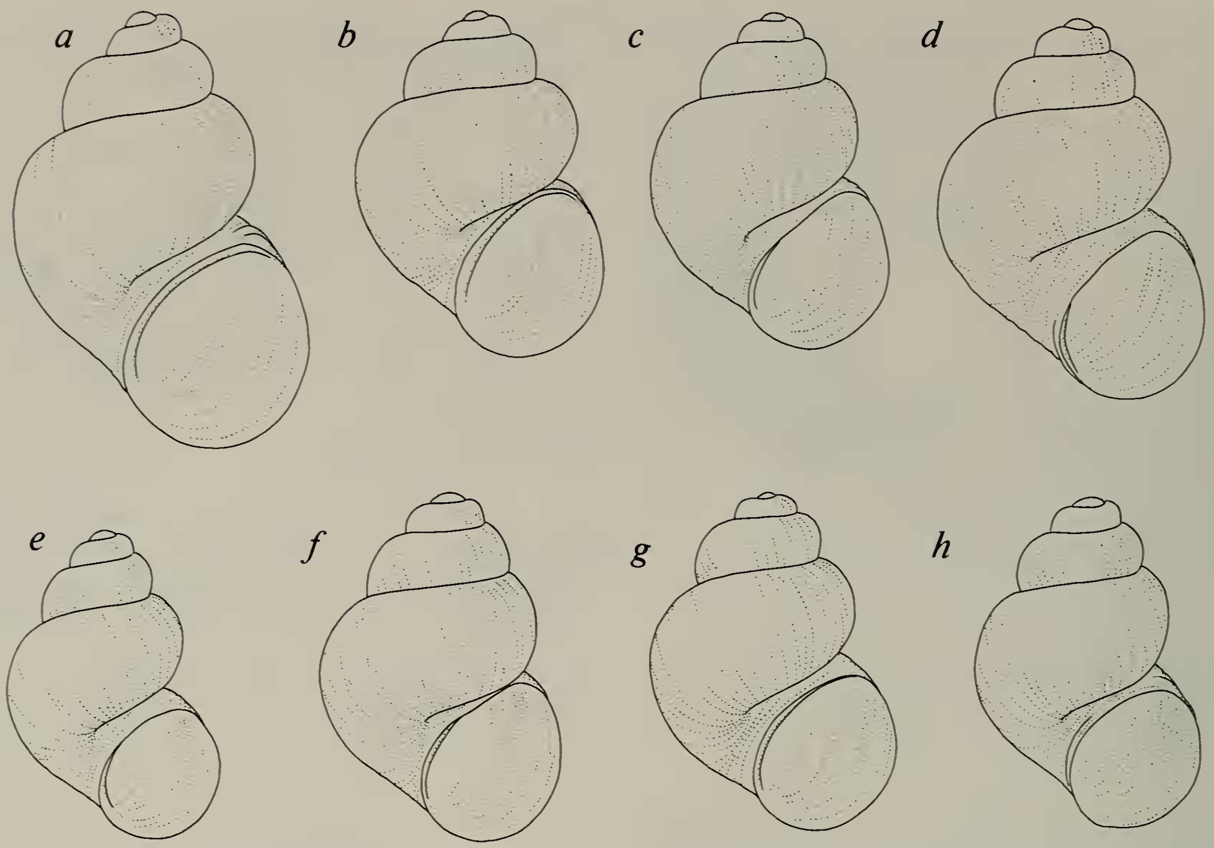

Fig. 20. Camera lucida drawings of shells of *P. micrococcus*: a, USNM 857936, Cane Spring (2.24 mm); b, USNM 853501, Shoshone Spring (1.96 mm); c, USNM 853502, Tecopa Hot Springs (1.90 mm); d, USNM 853506, Grapevine Springs (2.16 mm); e, USNM 853508, Hanaupah Spring (2.26 mm); f, USNM 853510, Saline Marsh (1.96 mm); g, USNM 853512, spring above Darwin Falls (1.94 mm); h, USNM 857937, Surprise Canyon stream (1.88 mm).

Type locality.—Near Oakland, Alameda County, California.

Distribution and habitat.—Distribution given by Taylor (1981:152) as "Central California, from Sonoma County to Monterey County along the coast, and inland in the foothills of the Sierra Nevada." Found in the study area in two moderate-sized, cool streams (16–20°C, 550 micromhos/cm) separated by 25 km along eastern slope of Sierra Nevada in Indian Wells Valley (Fig. 40). Snails common in watercress and *Chara*.

Remarks.—Shells of the Indian Wells Valley snails closely resemble *P. stearnsiana* from the San Francisco Bay area and their penes conform to a general description for the species provided by Gregg and Taylor (1965:107). Additional study, including examination of anatomy of topotypes or near-topotypes, will be necessary to confirm identity of the snails from Indian Wells Valley.

Pyrgulopsis wongi, new species
Wong's springsnail
Figs. 41–47

Material examined.—California: Inyo. Co.; Spring at Little Lake, east of HW 395 (10), USNM *853521, 9 Feb 1985.—Hogback Creek (Monache Mtn. quad.) (20), *853522, 28 Jun 1985, D. Wong.—Summit Creek (21), 853523, 12 Apr 1987.—Spring ca. 3.0 km north of Summit Creek (21), *853524, 12 Apr 1987.—Spring at Cabin Bar Ranch (25), 853525, 12 Oct 1987, J. Goldberg and M. Shumway.—Lubkin Creek (34), 853526, 16 Apr 1987.—Spring feeding Lubkin Creek (34), 857942, 25 Apr 1987.—Spring along east side of Tuttle Creek (35),

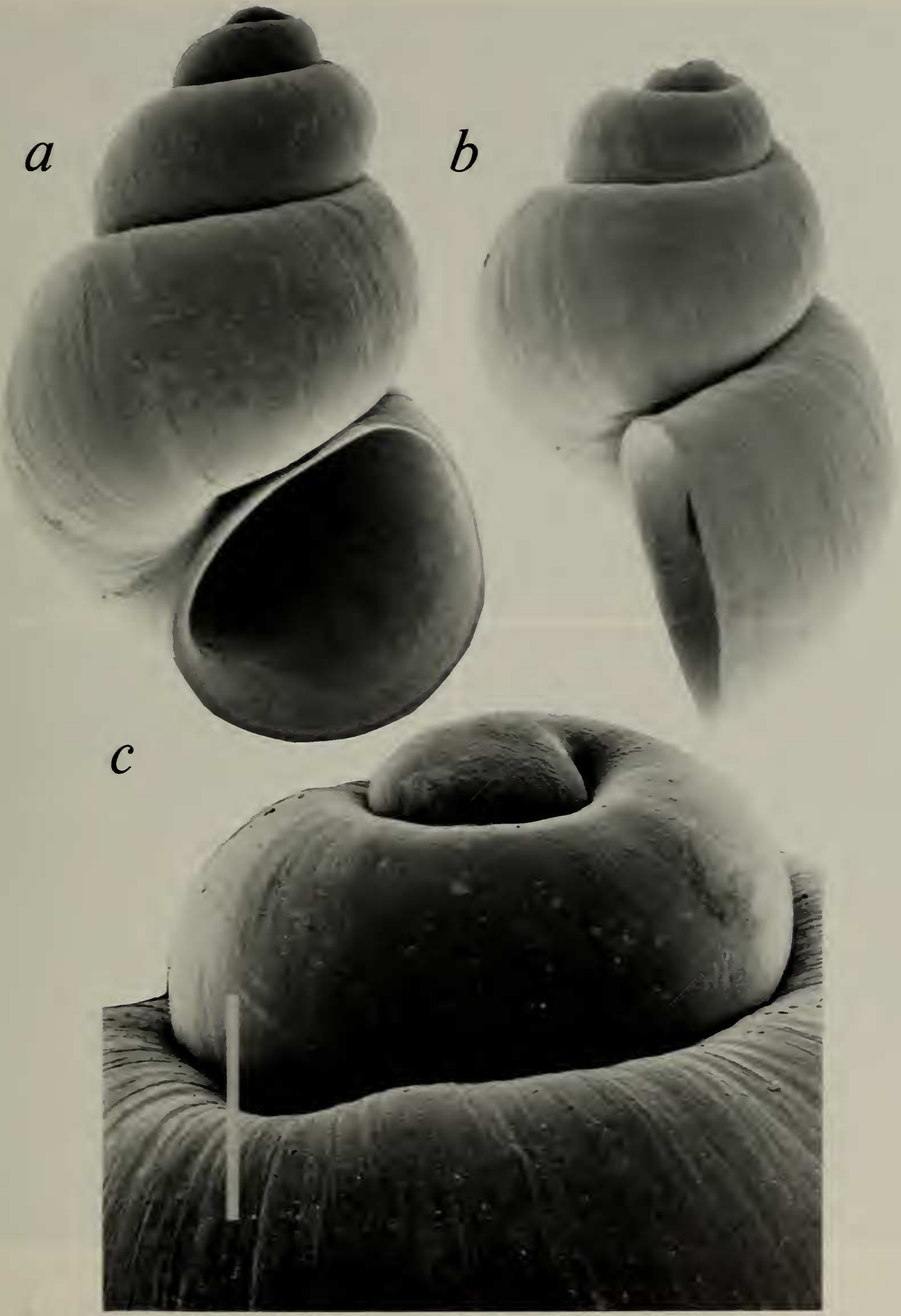

Fig. 21. SEM micrographs of *P. micrococcus*: a, USNM 853502, Tecopa Hot Springs (1.98 mm); b, USNM 853512, spring above Darwin Falls; c, USNM 853512, Tecopa Hot Springs (bar = 120 μm).

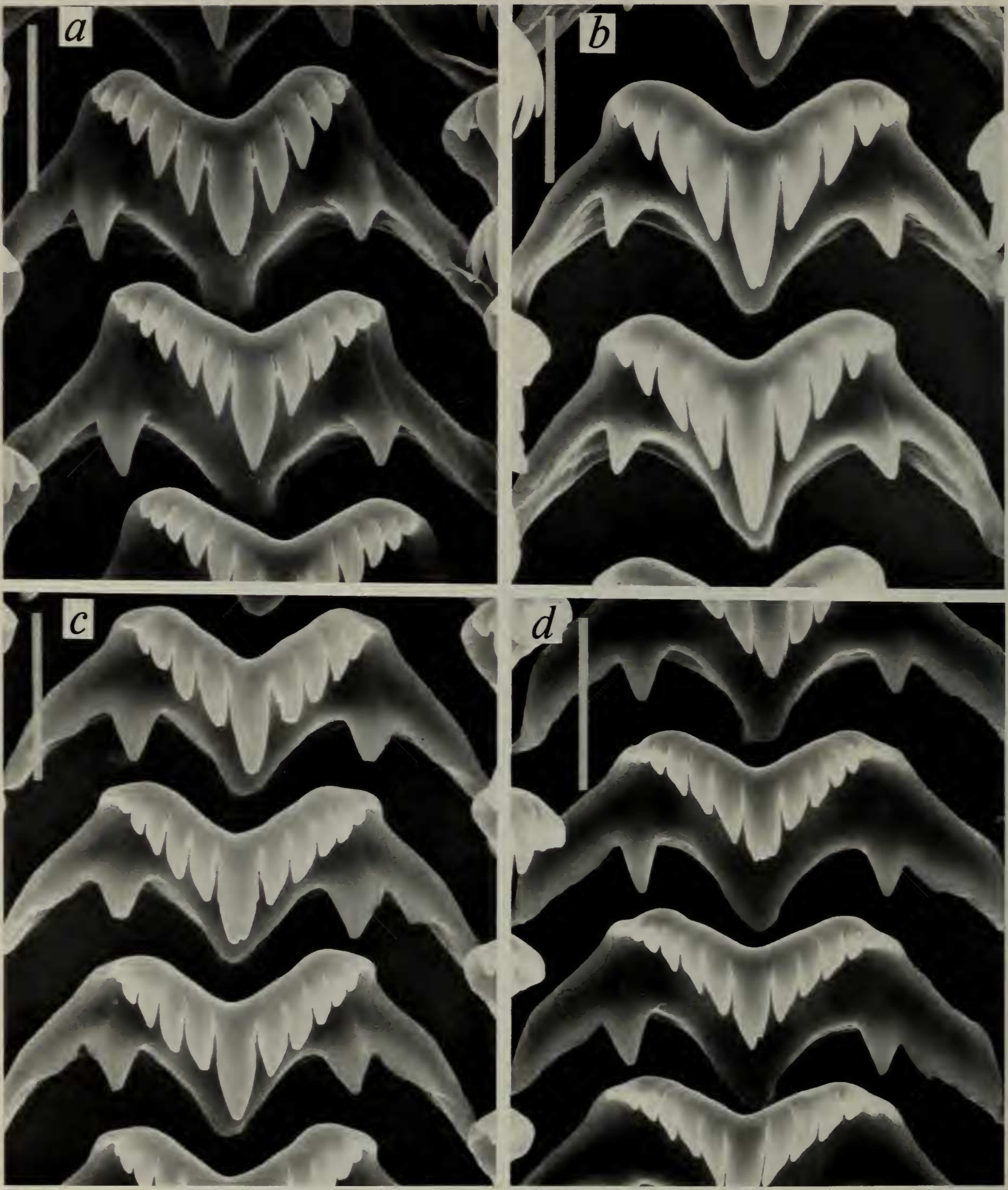

Fig. 22. Central radular teeth of *P. micrococcus*: a, USNM 857936, Cane Spring (bar = 7.5 μm); b, USNM 857963, Tecopa Hot Springs (bar = 7.5 μm); c, USNM 857965, spring E of Scotty's Castle (bar = 7.5 μm); d, USNM 857968, Saline Marsh (bar = 8.6 μm).

857943, 30 Apr 1987.—Hogback Creek (Lone Pine quad.) (36), *853527, 8 Feb 1985; 857976, 16 Apr 1987.—Boron Springs (40), *853528, 17 Apr 1987.—Stream in Charlie Canyon (43), *853529, 12 Jun 1987, D. Giuliani.—Spring on hill south of Warren Lake (57), *853530, 18 Apr 1987.—Spring in canyon south of Shannon Canyon (59), 857944, 20 Apr 1987.—Spring along north side of upper Pine Creek (69), *853531, 24

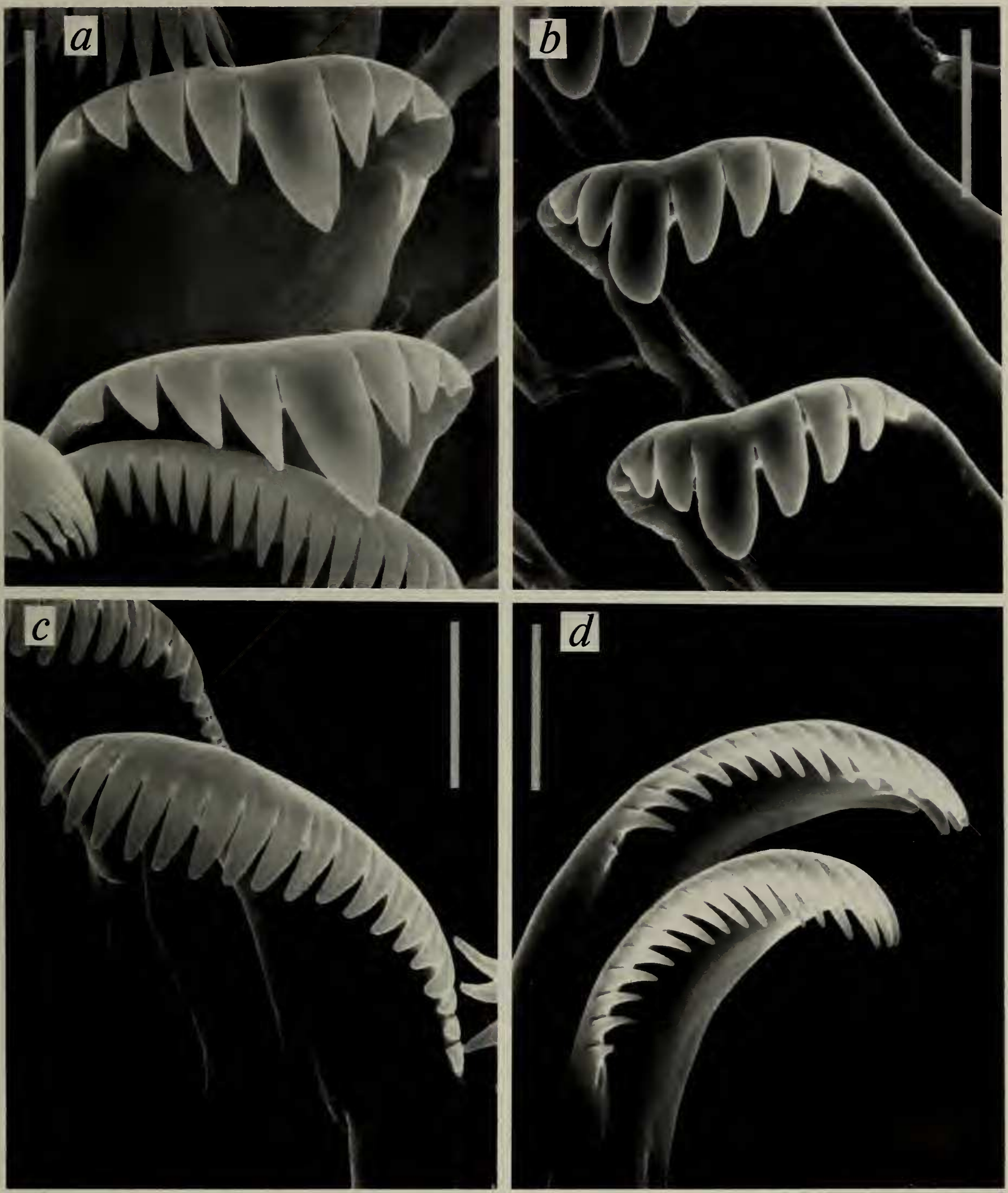

Fig. 23. Lateral and marginal radular teeth of *P. micrococcus*: a, Laterals, USNM 857936, Cane Spring (bar = 6.0 μm); b, Laterals, USNM 857966, Hanaupah Spring (bar = 7.5 μm); c, Inner marginals, USNM 857937, Surprise Canyon stream (bar = 5.0 μm); d, Outer marginals, USNM 857963, Tecopa Hot Springs (bar = 4.3 μm).

Apr 1987; 857977, 15 Sep 1987, D. Wong.—West spring in Birchim Canyon (70), 860403 (holotype), *857941 (paratypes), 3 May 1987.—East spring in Birchim Canyon (70), 857945, 3 May 1987.—Spring in Owens Gorge (74), *853532, 14 May 1985, D. Wong; 857978, 8 May 1987.—French Spring (89), *857947, 4 May 1987.—Barrel Springs

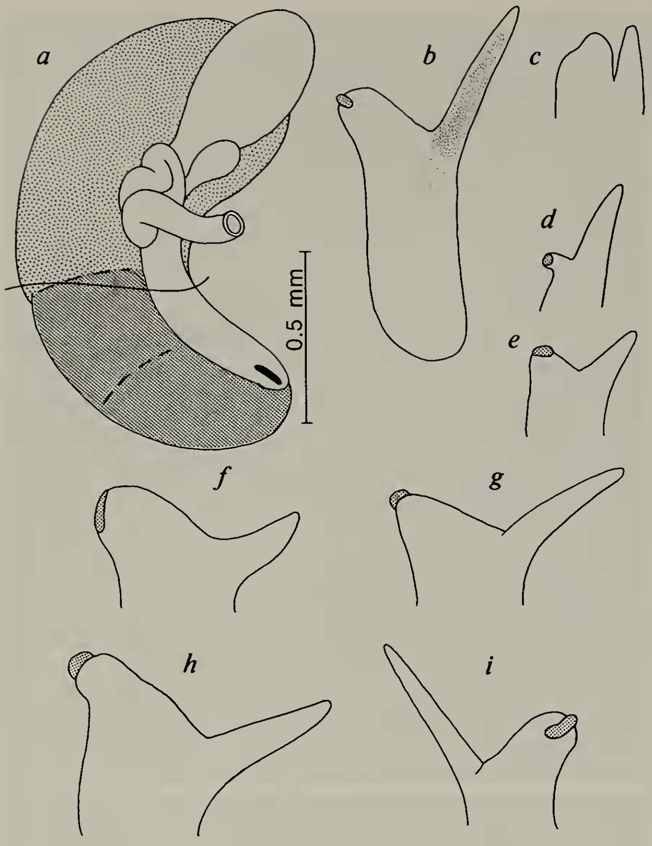

Fig. 24. Reproductive anatomy of *P. micrococcus*: a, Left lateral view of pallial oviduct complex, USNM 857961, spring in Oasis Valley; b–i, Penes (all dorsal except "i") (b, i, USNM 857936, Cane Spring; c, USNM 853505, Grapevine Springs; d, USNM 857962, Shoshone Spring; e, USNM 857963, Tecopa Hot Springs; f, USNM 857967, Johnson Canyon spring; g, USNM 857971, Tennessee Spring; h, USNM 853512, spring above Darwin Falls).

(91), *857948, 18 Aug 1987.—Spring at Toll House (97), *857949, 26 Apr 1987.—Corral Springs (160), *853535, 8 Feb 1985; 857979, 29 Mar 1987.—Antelope Spring (162), *853536, 8 Feb 1985. Mono Co.; Spring along Marble Creek (82), *853533, 22 Apr 1987.—Springs at north end of Blind Spring Valley (86); North Spring, *857946, 21 Apr 1987; South spring, 853534, 21 Apr 1987.—Layton Springs (122), *853537, 6 Feb 1985; 857980, 23 Apr 1987.—River Springs (132), *853538, 6 Feb 1985; 857981, 21 Apr 1987.

Diagnosis.—A small- to moderate-sized species with globose to low conical shell. Penis massive, with large filament and moderate-sized lobe. Ventral penis with two prominent swellings bearing glandular ridges. Glandular ridges, 7–12.

Description.—Shell (Figs. 41, 42) 1.2–3.0 mm high, height/width, 100–160%. Whorls, 3.25–4.5, well rounded, with slightly angulated shoulders. Body whorl 76–87% of shell height. Aperture broadly ovate, angled above. Apertural plane slightly tilted relative to coiling axis (Fig. 42c). Inner lip slightly thickened, usually only minimally reflected, either adnate to portion of or slightly separated from body whorl. Outer lip straight, thin. Umbilicus chink-like to moderately open.

Dark grey-black epithelial pigment on snout, proximal tentacles, and peripheral portions of sides of head/foot. Entirety of head/foot often very dark. Central portions of sides of head/foot usually with densely clustered dark, subepithelial pigment granules.

Radular (Figs. 43, 44) formula: (4–7)–1–(4–7)/1–1, (2–5)–1–(3–6), 17–26, 20–34 (from numerous populations). Central tooth relatively square-shaped; basal process well-excavated. Penis (Figs. 45b–l, 46) flattened, longer than wide. Filament fairly broad, short relative to length of remaining penis. Lobe slightly shorter than filament, broad, often widening distally. Glandular ridge arrangement typically as follows: 1) elongate ridge lining edge of lobe; 2) similar, stalked ridge on ventral surface just proximal to lobe; 3) similar ridge (rarely very reduced) on fleshy projection of ventral surface proximal to above; 4) elongate ridge covering proximal-most two-thirds of dorsal filament; 5) very elongate ridge on dorsal surface curving from just proximal to filament to lobe; 6) shorter ridges on dorsal surface along right side of (5) and in area between base of filament and edge of lobe. Modifications of above include addition of a few small ridges on central dorsal surface, addition of a single small ridge (sometimes stalked) on ventral surface, apparent fragmentation of ridges (particularly "1," "5"); apparent merging of adjacent ridges on dorsal surface. Filament darkened with sub-epithelial pigment along most of length. Capsule gland sub-equal to albumen gland (Fig.

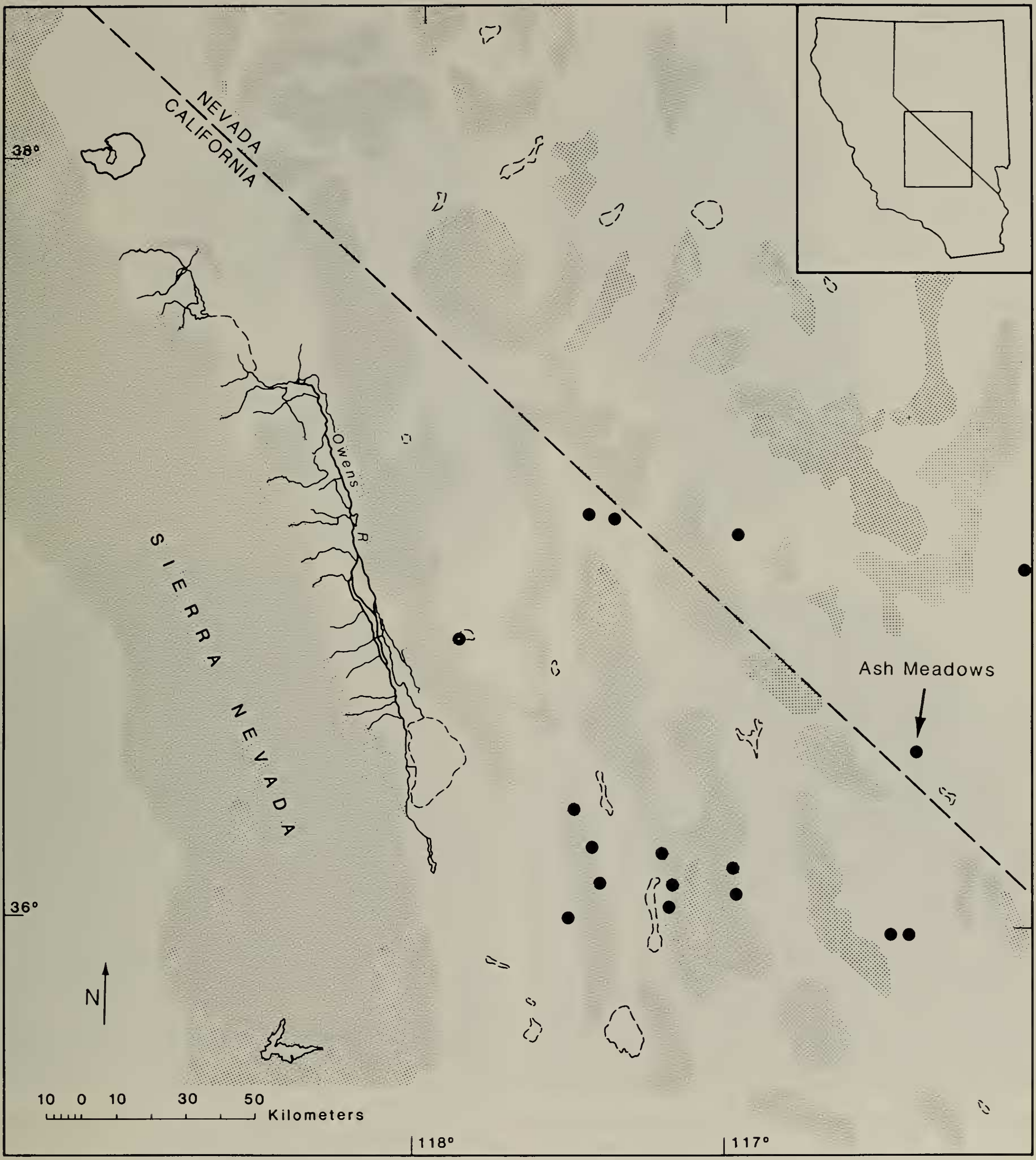

Fig. 25. Map showing distribution of *P. micrococcus*. Snail occurs at 15 localities in Ash Meadows.

45a). Seminal receptacle small, positioned lateral to anterior bursa copulatrix. Bursa pear-shaped, massive, with about one-third of length posterior to albumen gland.

Type locality.—Spring in Birchim Canyon north of Bishop, Inyo Co., California.

Distribution and habitat.—Widespread in Owens Valley along eastern escarpment of Sierra Nevada from Pine Creek south to Little Lake, and along western side of valley from French Spring to Marble Creek. Also found in a few sites in Long, Adobe, and Deep Springs Valleys (Fig. 47). Habitat includes seeps and spring-fed streams of small-moderate size (9.5–22°C, 85–450 micromhos/cm) (Fig. 9b, c). Snails typically common in watercress and/or on small bits of travertine and stone.

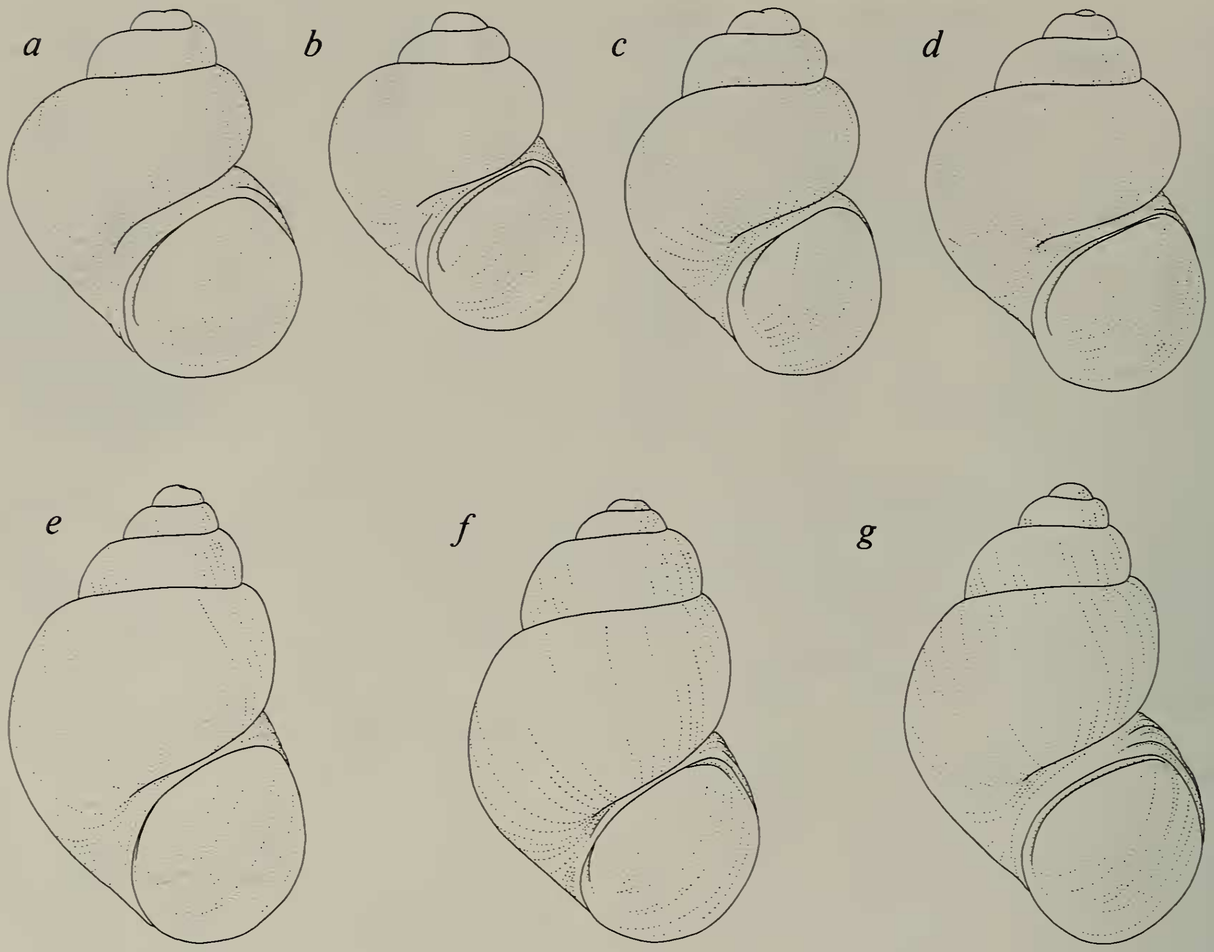

Fig. 26. Camera lucida drawings of shells of *P. owensensis* and *P. perturbata*: a–d, *P. owensensis* (a, USNM 853540, Mule Spring [2.1 mm]; b, USNM 857950, spring at Toll House [2.3 mm]; c, USNM 857955, stream in canyon S of Piute Creek [2.08 mm]; d, USNM 853543, spring at Graham Ranch [2.16 mm]); e–g, *P. perturbata* (e, USNM 853546, Fish Slough, "Northwest Springs," [3.93 mm]; f, USNM 853549, Fish Slough, "BLM Spring," [3.22 mm]; g, USNM 853548, Fish Slough, "NE Spring" [3.97 mm]).

Etymology.—Named after Darrell Wong, California Fish and Game, for his assistance during the project and interest in conserving Owens Valley springsnails.

Remarks.—Similar in penial morphology to *P. californiensis* (Gregg & Taylor) from western California (Taylor 1981:154). Distinguished from above by globose shell, and more numerous stalked glandular ridges on ventral penial surface.

Genus *Tryonia* Stimpson, 1865
Tryonia margae, new species
Grapevine Springs elongate tryonia
Figs. 48–50, 51a, 52

Material examined.—California: Inyo Co.; Grapevine Springs (241); (upper) Warm spring on limestone bench, USNM 860408 (holotype), *857952 (paratypes), 14 Mar 1987; Spring on limestone bench above ranch 853555, 25 Feb 1987; 857996, 14 Mar 1987.

Diagnosis.—A small-sized species with narrow, turriform shell. Penis small, with 3 papillae on inner curvature, and a single papilla (sometimes absent) on outer curvature. Distal tip of penis with elongate swelling on inner side.

Description.—Shell (Fig. 48) 1.5–2.9 mm high, height/width, 250–300%. Whorls, 4.5–6.25, rounded, with angulated shoulders. Sutures often deeply impressed. Apex blunt, protoconch slightly depressed (Fig. 48g).

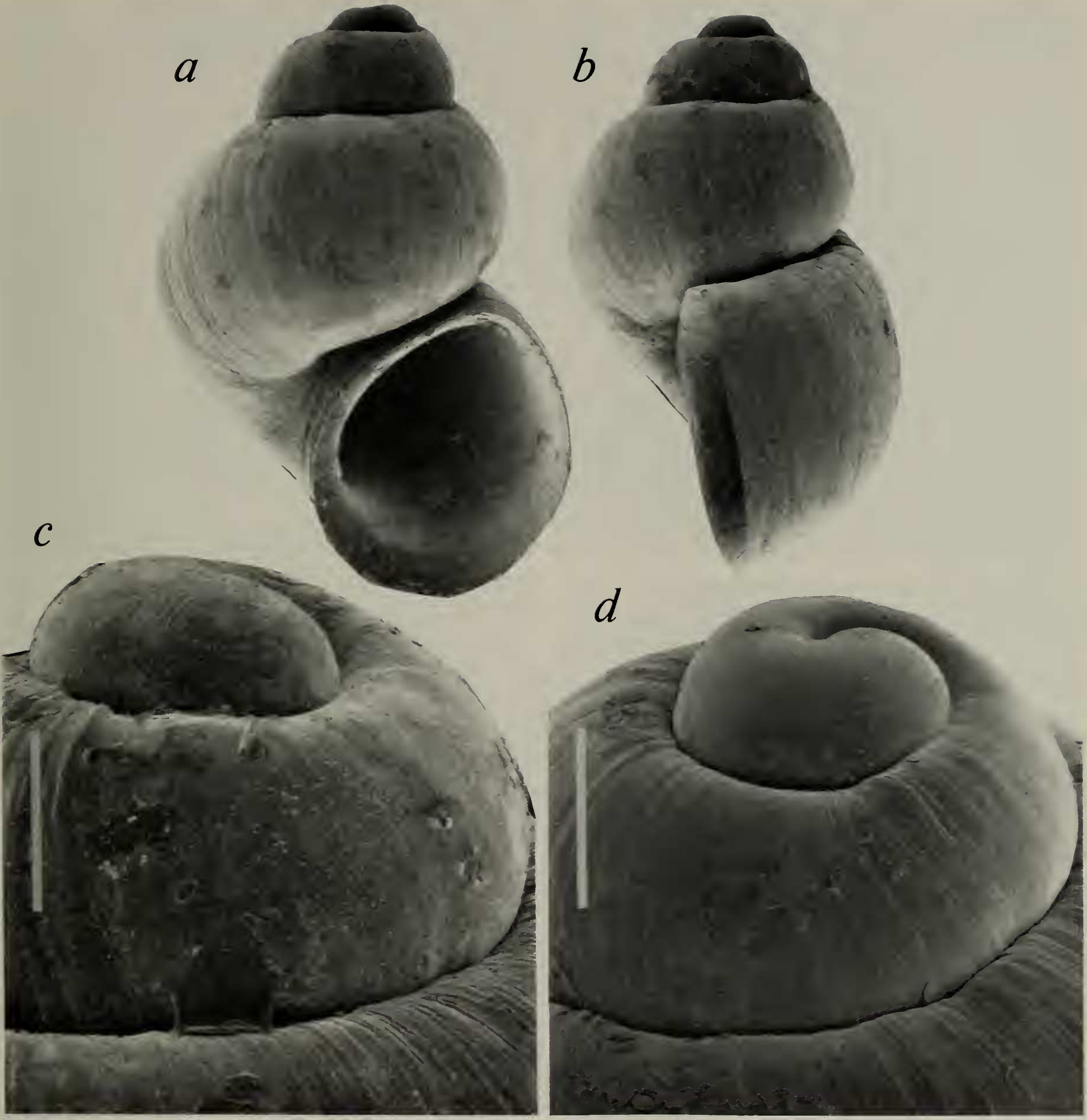

Fig. 27. SEM micrographs of *P. owensensis* from stream in canyon S of Piute Creek: a, Holotype, USNM 860404 (2.0 mm); b–d, Paratypes, USNM 857955 (bars = 120 μm, 176 μm).

Body whorl 45–55% of shell height. Marl frequently covering apical whorls, with near-entirety of shell sometimes blanketed. Aperture narrowly ovate. Inner lip well-reflected, slightly thickened, adnate to or slightly separated from body whorl. Outer lip sinuate, thin (Fig. 48d, f). Umbilicus chink-like. Protoconch near-smooth (Fig. 48g). Collabral growth lines well developed on teleoconch, often elevated at irregular intervals. Spiral sculpture consisting of weak striations.

Dark brown-black epithelial pigment covering most of head/foot, although sometimes absent on tentacles, and lighter on snout and central portion of sides of "neck."

Radular (Figs. 49, 50) formula: 4(5)–1–4(5)/1(2)–1(2), 2(3)–1–3(4), 20–21, 22–28.

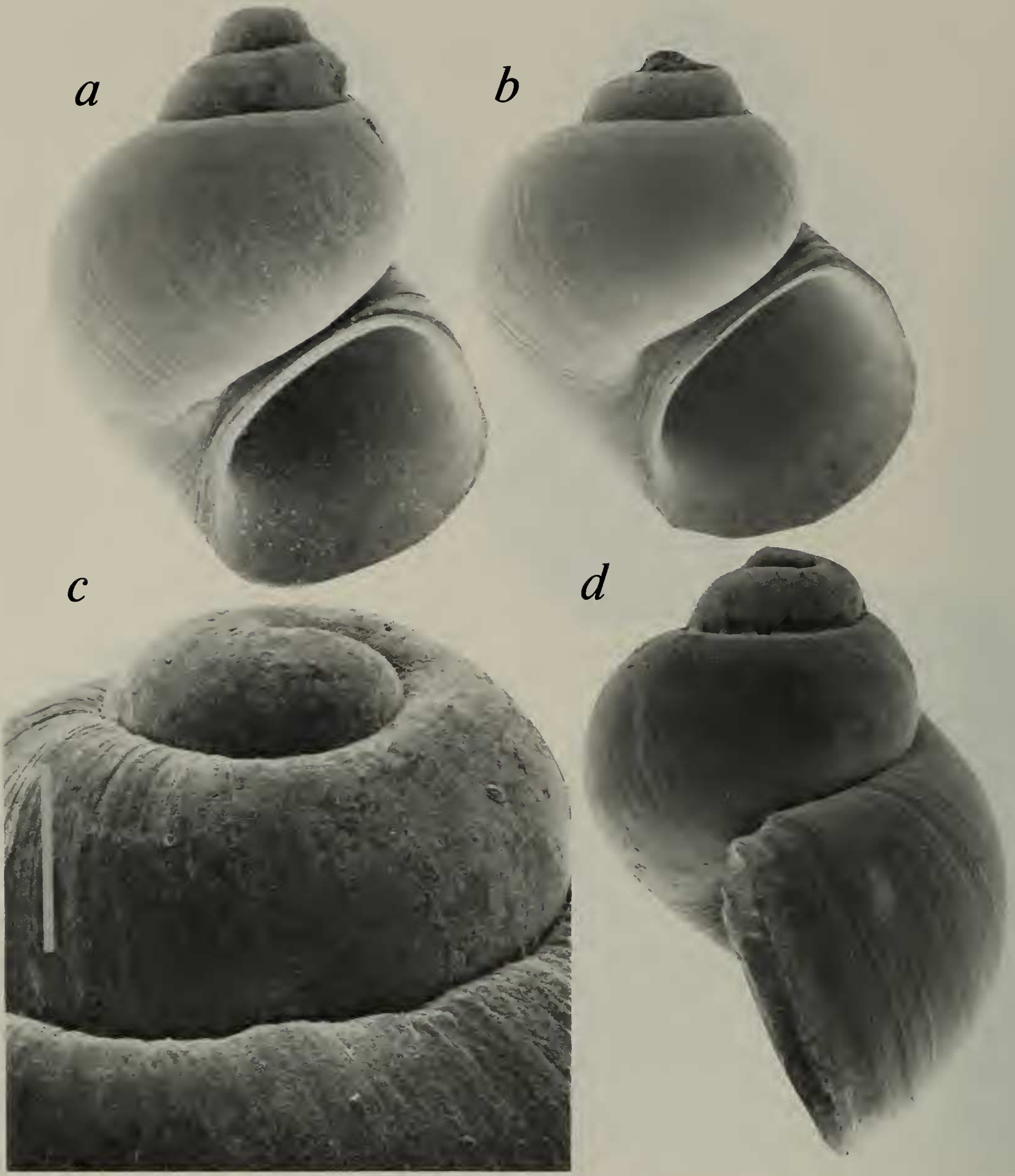

Fig. 28. SEM micrographs of *P. owensensis* from Warm Springs: a (1.92 mm), b, d, USNM 853544, main spring; c, USNM 853545, spring N of above (bar = 136 μm).

Central tooth broadly trapezoidal, basal cusps large, basal process well excavated. Central cusps of lateral tooth only slightly enlarged (Fig. 49c, d). Penis (Fig. 51a) extending only slightly beyond edge of mantle collar. Enlarged papilla located on outer edge of penis at base. Two smaller papillae positioned along distal half on inner edge; similar small papilla usually found near base on inner edge. Brown-black epithelial pigment usually prominent near distal tip, at bases of two distal papillae. Lighter pigment dusting much of dorsal surfaces of penis and 2 proximal papillae.

Type locality.—Warm spring on limestone bench in Grapevine Springs complex, northern Death Valley, Inyo Co., California.

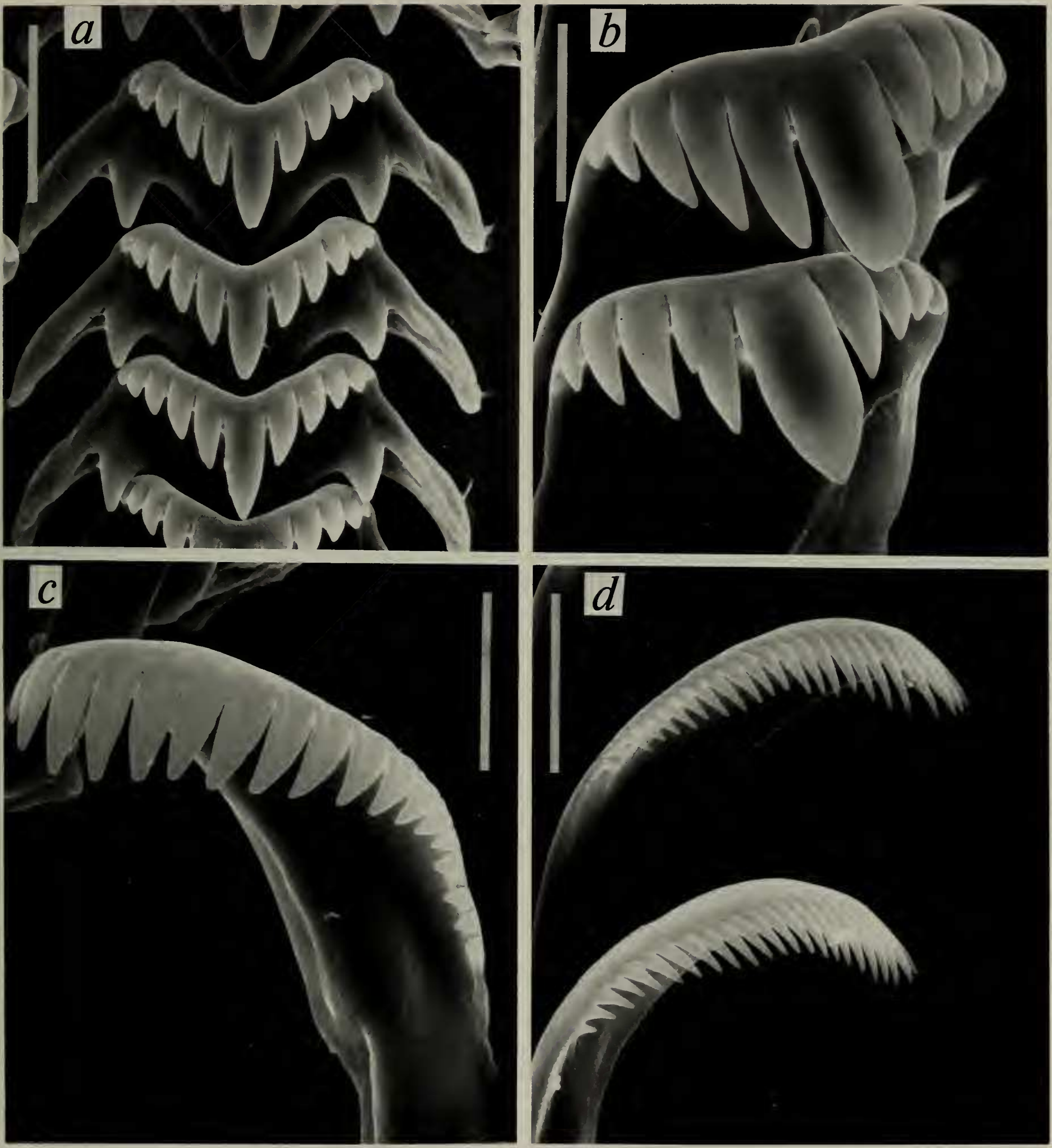

Fig. 29. Radula of *P. owensensis,* USNM 857955, stream in canyon S of Piute Creek: a, Centrals (bar = 10 μm); b, Laterals (bar = 6.7 μm); c, Inner marginal (bar = 6.0 μm); d, Outer marginals (bar = 6.0 μm).

Distribution and habitat.—Found in two sites (separated by about 1 km) among Grapevine Springs in northern Death Valley (Fig. 52). Habitat consists of upper portions of shallow spring brooks flowing over travertine (Fig. 8b), on which snails were moderately common. Springs were highly mineralized (1050–1075 micromhos/cm), but differed considerably in temperature (west spring, 26–27°C; east, 36–37°C). Syntopic with *T. rowlandsi* in the thermal spring.

Etymology.—From Latin *marga,* meaning marl, and referring to occurrence of snail in travertine springs.

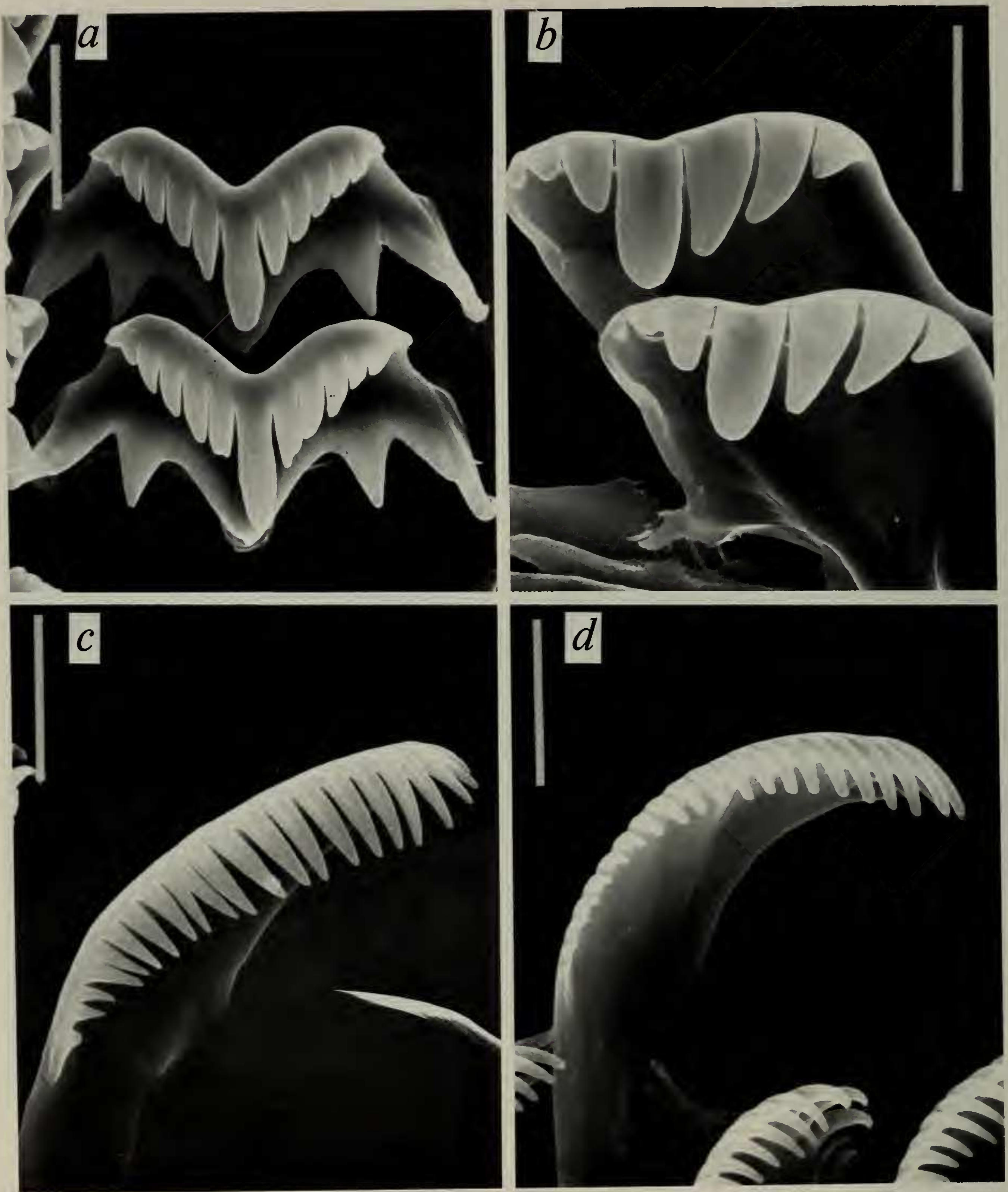

Fig. 30. Radula of *P. owensensis,* USNM 857988, Warm Springs (main spring): a, Centrals (bar = 6.7 μm); b, Laterals (bar = 6.0 μm); c, Inner marginal (bar = 6.0 μm); d, Outer marginals (bar = 3.8 μm).

Tryonia protea (Gould, 1855)
Desert tryonia
Figs. 52–54

Amnicola protea Gould 1855:129.
Melania exigua Conrad 1855:269.
Pyrgulopsis blakeana Taylor 1950:30.
Pyrgulopsis cahuillarum Taylor 1950:31.

Material examined.—California: Mono Co.; Hot Creek, USNM *857954, 23 Apr 1987.

Diagnosis.—A moderate to large-sized species (shell height typically 3–7 mm) with elongate-conic to turriform shell. Shell smooth or with spiral and/or collabral sculpture varying from faint striations to elevated ridges.

Description of Hot Creek population.—Shell (Fig. 53) 3.0–4.5 mm high, height/width, 210–242%. Whorls, 4.75–6.25, rounded. Sutures moderately impressed. Body whorl 55–61% of shell height. Protoconch slightly depressed (Fig. 53b), apex of adults invariably highly eroded. Aperture ovate, apertural plane tilted relative to coiling axis. Inner lip only slightly thickened and reflected, broadly adnate to body whorl. Outer lip thin, slightly sinuate. Umbilicus chink-like, near-absent. Smooth surface of protoconch lined with well-spaced rows of numerous, shallow perforations (Fig. 53b, c). Teleoconch with strong growth lines; 10–20 spiral lines prominent on middle whorls, sometimes extending to aperture.

Brown epithelial pigment dense on most of snout. Black patches of subepithelial pigment along edges of sides of head/foot. Pallial roof with paired, black pigment patches extending along length of ctenidium.

Radular (Fig. 54) formula: 5(6)–1–5(6)/2(3)–2(3), (3–5)–1–(6–8), 35–36, 28–31 (from single population). Central tooth broadly trapezoidal; basal cusps large, basal process moderately excavated. No males found among the more than 100 specimens collected.

Type locality.—Colorado Desert (probably in Riverside County, California [based on Blake 1857]).

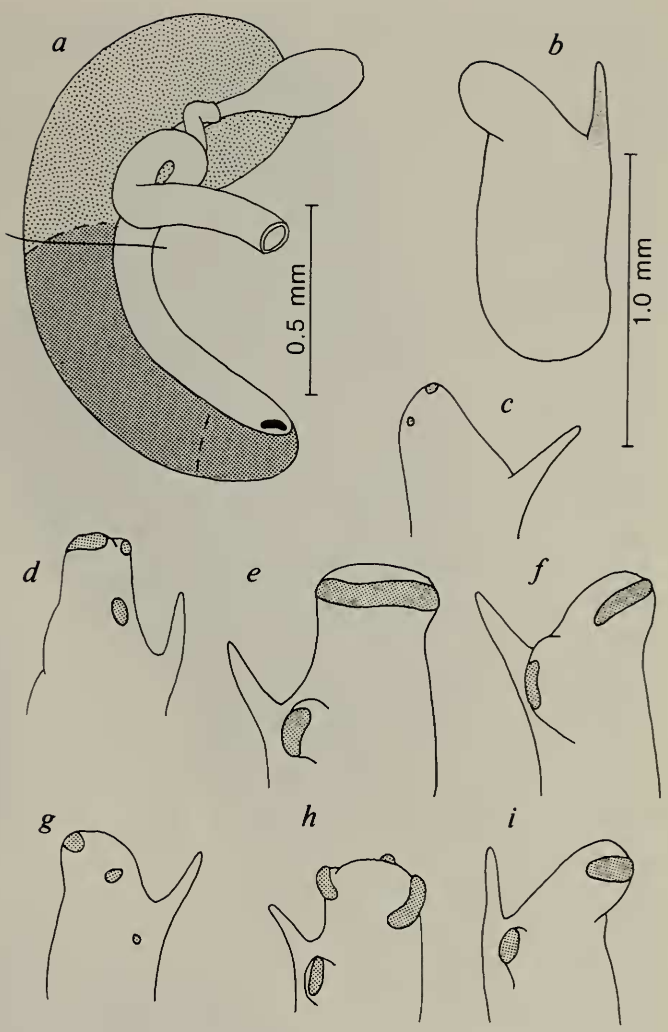

Fig. 31. Reproductive anatomy of *P. owensensis*: a, Left lateral view of pallial oviduct complex, USNM 857955, stream in canyon S of Piute Creek; b–i, Penes (b [dorsal], i [ventral], USNM 857955, stream in canyon S of Piute Creek; c [dorsal], f [ventral], USNM 857983, Mule Spring; d [dorsal], g [ventral], h [ventral], USNM 857988, Warm Spring (main spring); e [ventral], USNM 857989, Warm Springs [spring N of above]). "b" through "i" drawn to same scale.

Distribution and habitat.—"Western Utah to southeastern California, adjacent Baja California, and southeastern Arizona" (Taylor 1981:155), with only two living populations known from California: that of Hot Creek (Fig. 52) and Dos Palmas Spring in Riverside County (Taylor 1981:154). At Hot Creek (Fig. 9d), snails were rare on various submergent macrophytes lining sides

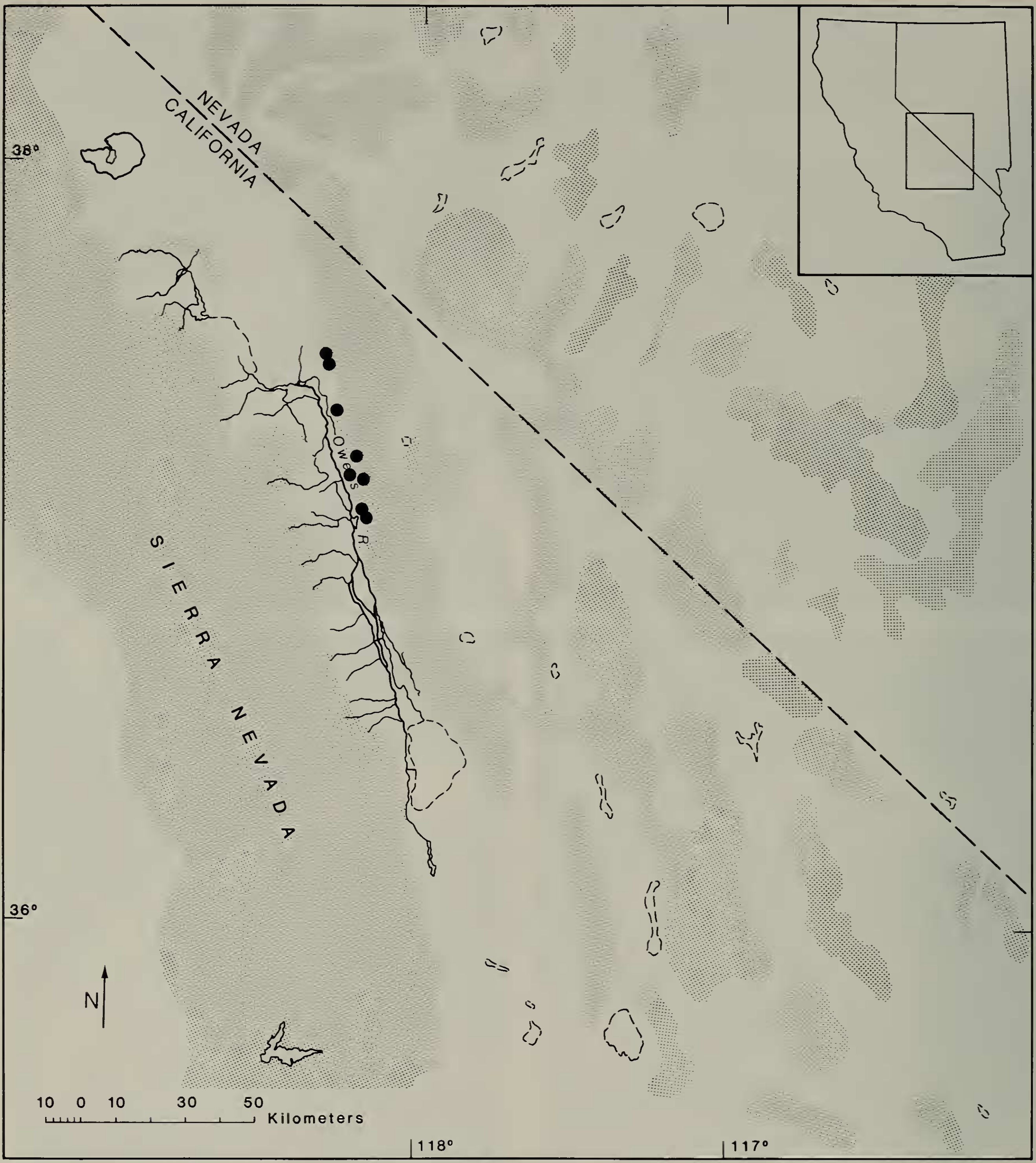

Fig. 32. Map showing distribution of *P. owensensis.*

of the swiftly flowing thermal stream (32°C, 480 micromhos/cm).

Remarks.—The taxonomic concept of this form is vague (Taylor 1966:53–54) and status of the few living (and mostly widely separated) populations (Taylor 1985:fig. 35) remains unclear. The Hot Creek population is referable to *T. protea* on basis of shell form, size, and sculpture, but confirmation by anatomical comparison with snails from Dos Palmas Spring (that represent near topotypes) would be desirable.

Tryonia robusta, new species
Robust tryonia
Figs. 51d, 52, 55–58

Material examined.—California: Inyo Co.; Nevares Springs (230); Spring on trav-

Fig. 33. SEM micrographs of *P. perturbata* from Fish Slough, "Northwest Springs," south spring: a, b, Holotype, USNM 860407 (3.57 mm); c, Paratype, USNM 853456 (bar = 200 μm).

ertine mound, USNM 860411 (holotype), *853557 (paratypes), 2 Feb 1985; 857999, 16 Nov 1985; 857958, 12 Mar 1987; Spring issuing from base of mound, 853558, 2 Feb 1985—Travertine Springs; South spring, *853559, 2 Feb 1985; 857959, 12 Mar 1987; North spring, 857960, 12 Mar 1987.

Diagnosis.—A small-sized species with

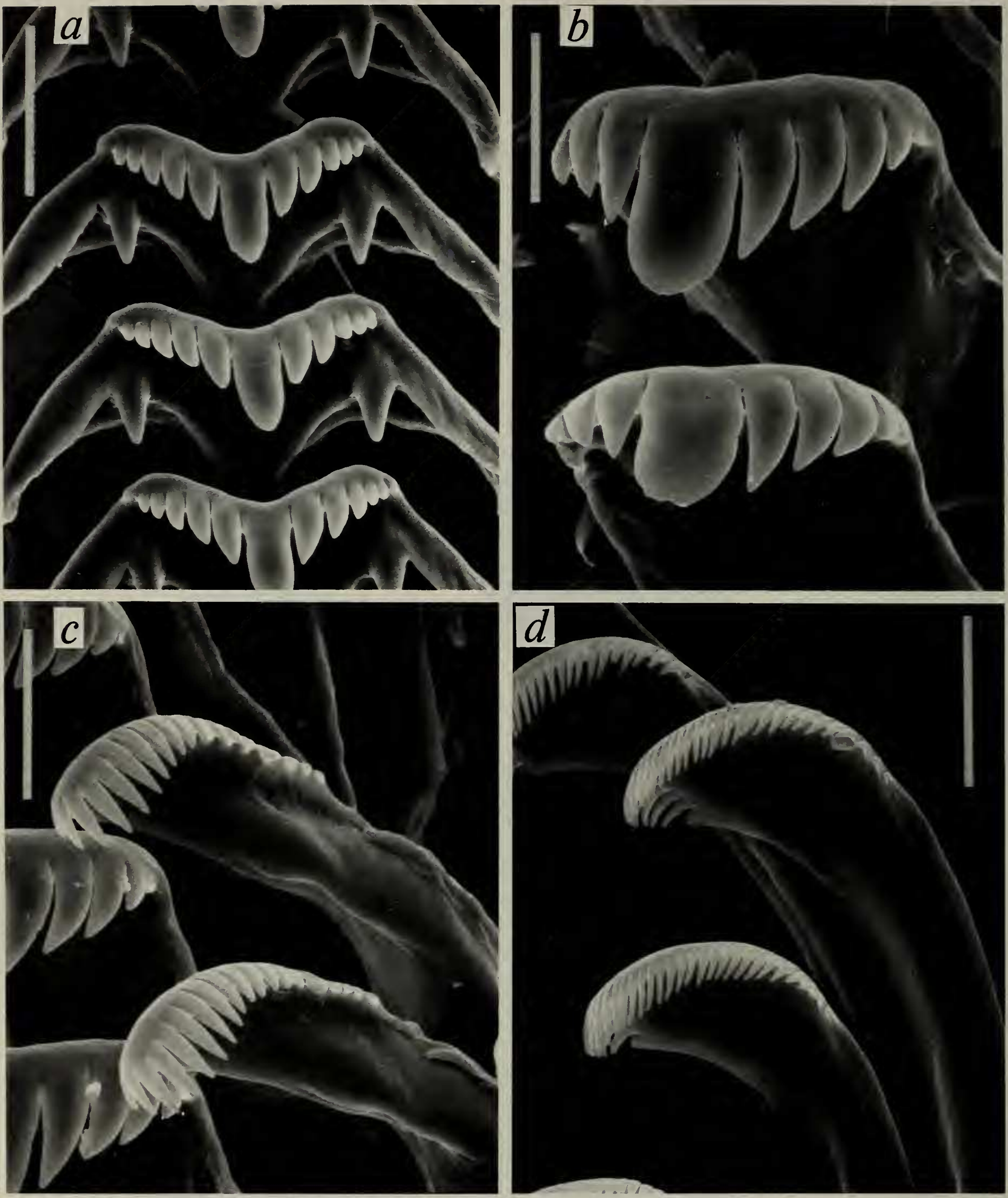

Fig. 34. Radula of *P. perturbata,* USNM 857990, Fish Slough, "Northwest Springs," south spring: a, Centrals (bar = 13.6 μm); b, Laterals (bar = 10 μm); c, Laterals and inner marginals (bar = 12 μm); d, Outer marginals (bar = 10 μm).

unusually broadly conical shell for genus. Penis moderate-sized, with single papilla on outer curvature.

Description.—Shell (Fig. 55) 1.1–2.1 mm high, height/width, 140–170%. Whorls, 3.75–4.75, rounded, with pronounced shoulders. Sutures impressed. Body whorl 68–80% of shell height. Protoconch (Figs.

56a–c) simple, sometimes eroded. Aperture near-ovate, sometimes sharply angled above; apertural plane slightly tilted relative to coiling axis. Inner lip thickened, moderately reflected, usually slightly separated from body whorl. Outer lip thin, near-straight. Umbilicus chink-like. Protoconch surface wrinkled (Figs. 56a–c). Teleoconch often with weak spiral striations, particularly on upper whorls.

Operculum (Fig. 56d) thin, paucispiral, with 2.5–3.0 rapidly expanding whorls.

Brown-black melanic pigment dark on snout and posterior edge of "neck," variable on central portions of sides of head/foot; sub-epithelial pigment granules prominent in latter. Mantle roof epithelial pigment typically uniformly dark brown-black.

Radular (Fig. 57) formula: (5–7)–1–(5–7)/1–1, 3(4)–1–5(6), 24, 22–27 (from two populations). Central tooth relatively square-shaped; central cusps elongate, basal cusps small, basal process highly excavated. Cephalic tentacles covered with sparse, irregular patches of hypertrophied cilia, rarely forming short tracts. Penis (Figs. 51d, 58) considerably longer than wide, moderately thickened. Attachment area broad, with rest of narrow length coiled in tight, clockwise fashion. Papilla small, conical, positioned along outer curvature just proximal to mid-length. Distal tip blunt, with inner side slightly swollen; surface of tip densely covered with elongate cilia. Distal tip of papilla simple, lightly ciliated (Fig. 58b).

Type locality.—Nevares Springs, Death Valley, Inyo County, California.

Distribution and habitat.—Found at Nevares and Travertine Springs along base of Funeral Mountains in mid-eastern Death Valley (Fig. 52). Snails found commonly on plant debris and travertine in shallow outflows of four thermal springs (30–37°C, 900–975 micromhos/cm). Extinct at Texas Springs (located between above complexes).

Etymology.—Referring to unusually broad shell for genus.

Remarks.—Shell form and penial shape and lobation pattern are highly distinctive, and relationship between this local endemic and other congeners in region is unclear. Species closely conforms to typical *Tryonia* in other features (including details of female reproductive morphology).

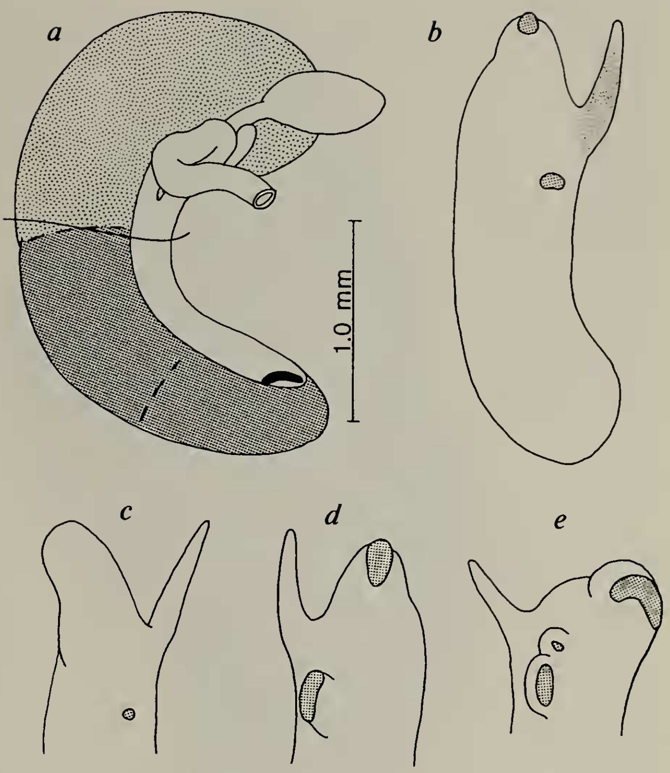

Fig. 35. Reproductive anatomy of *P. perturbata* from Fish Slough, " Northwest Springs": a, Left lateral view of pallial oviduct complex, USNM 857990, south spring; b–e, Penes (b [dorsal], c [dorsal], d [ventral], USNM 857990, south spring; e [ventral], USNM 857991, north spring).

Tryonia rowlandsi, new species
Grapevine Springs squat tryonia
Figs. 51b, 52, 59, 60

Material examined.—California: Inyo Co.; Grapevine Springs (241); (upper) Warm spring on limestone bench, USNM 860409 (holotype), *857953 (paratypes), 14 Mar 1987; (lower) Warm spring on limestone bench, 857997, 14 Mar 1987.

Diagnosis.—A small-sized species with elongate-conic shell. Penis large, with single papilla on outside curvature and 2 papillae on inside curvature.

Description.—Shell (Fig. 59) 1.7–2.3 mm

Fig. 36. Map showing distribution of *P. perturbata.*

high, height/width, 140–190%. Whorls, 4.0–4.75, rounded, somewhat shouldered. Sutures impressed. Body whorl 62–74% of shell height. Protoconch tilted relative to teleoconch. Aperture ovate, apertural plane slightly tilted relative to coiling axis. Inner lip thin, only very slightly reflected, adnate to or slightly separate from body whorl. Outer lip thin, near-straight. Umbilicus narrow, chink-like. Protoconch mottled with series of short, predominantly spiral striations (Fig. 59e). Teleoconch with weakly developed spiral lines, particularly on upper whorls.

Head/foot and visceral coil usually uniformly coated with dark brown epithelial

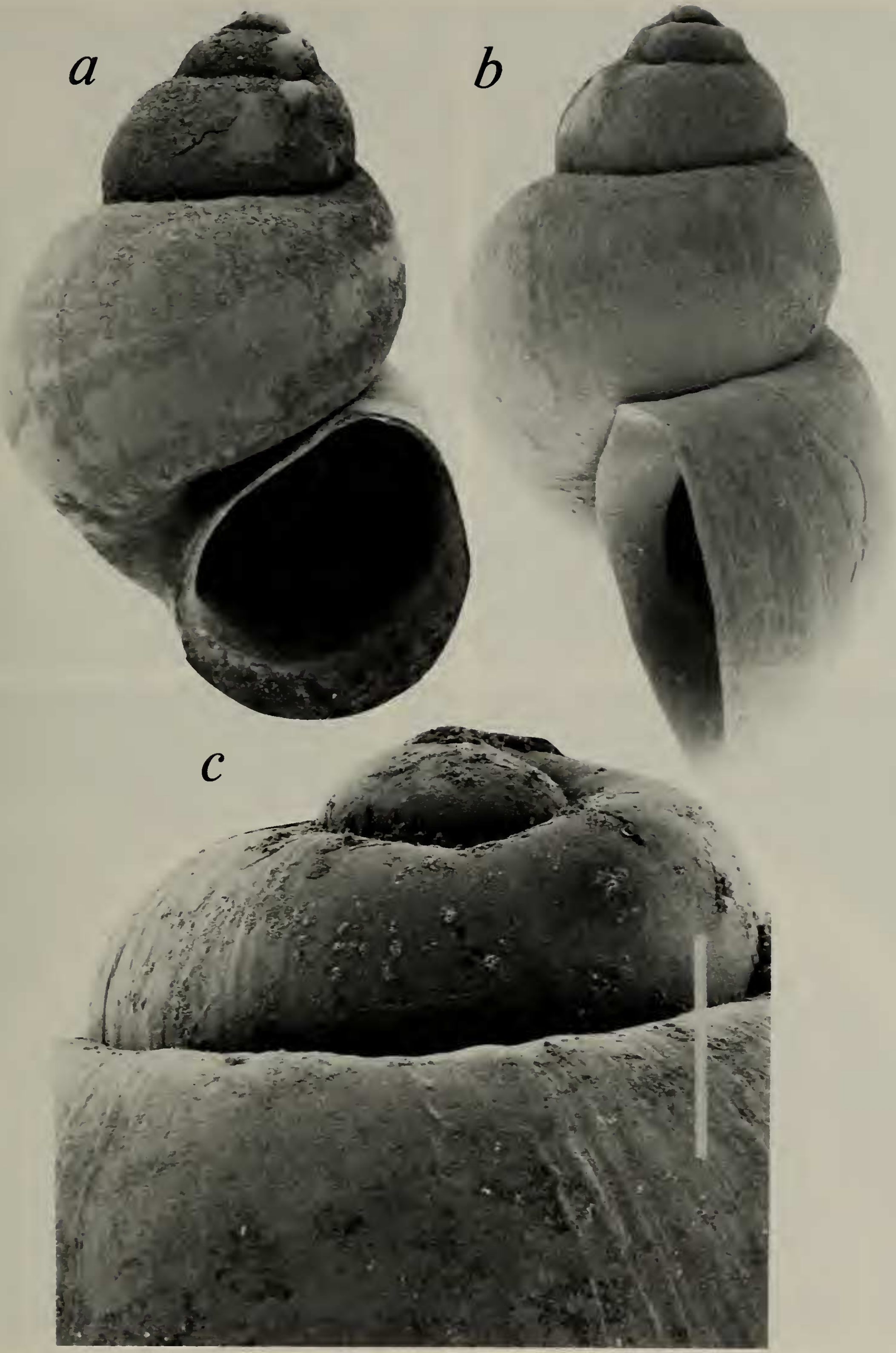

Fig. 37. SEM micrographs of *P.* cf. *stearnsiana,* USNM 853519, Sand Canyon (a, 3.04 mm; bar = 136 μm).

pigment. Central portions of sides of head/foot consisting of either a thin band or broad patch, often lighter or unpigmented.

Radular formula (Fig. 60): 4(5)–1–4/1(2)–1, 2(3)–1–2(3), 16, 20 (from paratypes). Central tooth broadly trapezoidal; basal cusps small, basal process only moderately excavated. Lateral tooth having unusual "claw-like" appearance, with cusps few and widely separated. Penis (Fig. 51b) elongate,

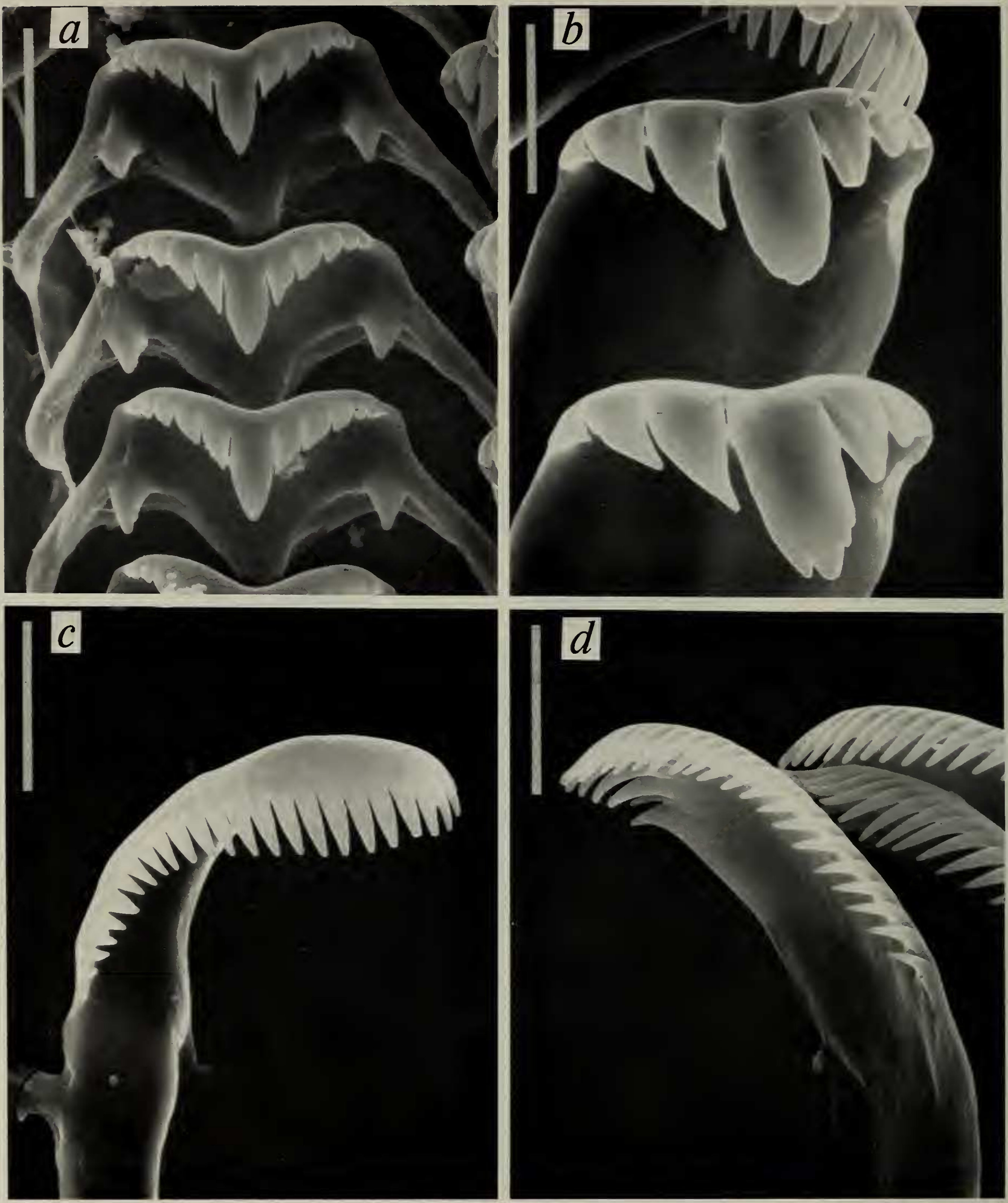

Fig. 38. Radula of *P.* cf. *stearnsiana,* USNM 857974, Sand Canyon: a, Centrals (bar = 10 μm); b, Laterals (bar = 6.0 μm); c, Inner marginal (bar = 8.6 μm); d, Outer marginals (bar = 6.0 μm).

distal tip with slightly swollen inner edge. Attachment area broad, with remaining penis near-totally uncoiled. Single, small papillae located on outer curvature near midpoint, and on inner curvature near distal tip. Inner curvature also bearing enlarged, basal papilla. Penial pigmentation consisting of small, dark patch near distal tip and/or light dusting on broad area near base.

Type locality.—Grapevine Springs,

Grapevine Mountains, Death Valley, Inyo Co., California.

Distribution and habitat.—Found in two thermal, highly mineralized springs on limestone bench in northeast portion of Grapevine Spring complex (32–36°C, 1100–1050 micromhos/cm) (Fig. 52).

Etymology.—Named after Peter Rowlands, Resources Management Division, National Park Service, Death Valley, for his efforts in both assisting this study and conserving local aquatic gastropods in the Monument.

Tryonia salina, new species

Cottonball Marsh tryonia
Figs. 51e, 52, 61, 62

Tryonia sp.—Taylor *in* LaBounty and Deacon 1972:775.

Material examined.—California: Inyo Co.; Spring in Cottonball Marsh (231), USNM 860410 (holotype), *853556 (paratypes), 22 Feb 1985; *857998, 11 Mar 1987.

Diagnosis.—A moderate-sized species with elongate-conic shell bearing well-developed spiral striae. Penis with three papillae on inner curvature and single papilla on outer curvature.

Description.—Shell (Fig. 61) 2.4–3.1 mm high, height/width, 150–190%. Whorls, 4.5–5.25, well-rounded, shouldered above. Sutures impressed. Shell loosely coiled, with slight separation of upper whorls common. Body whorl 61–68% of shell height. Protoconch tilted relative to teleoconch. Aperture ovate, apertural plane slightly tilted relative to coiling axis. Inner lip thin, only slightly reflected, narrowly adnate to or slightly separated from body whorl. Outer lip thin, near-straight. Umbilicus chink-like to moderately open. Protoconch smooth (Fig. 61c). Teleoconch with strong, regularly-spaced spiral striations, usually continuing onto body whorl, interacting with occasionally highly pronounced growth lines to produce a weakly cancellate appearance.

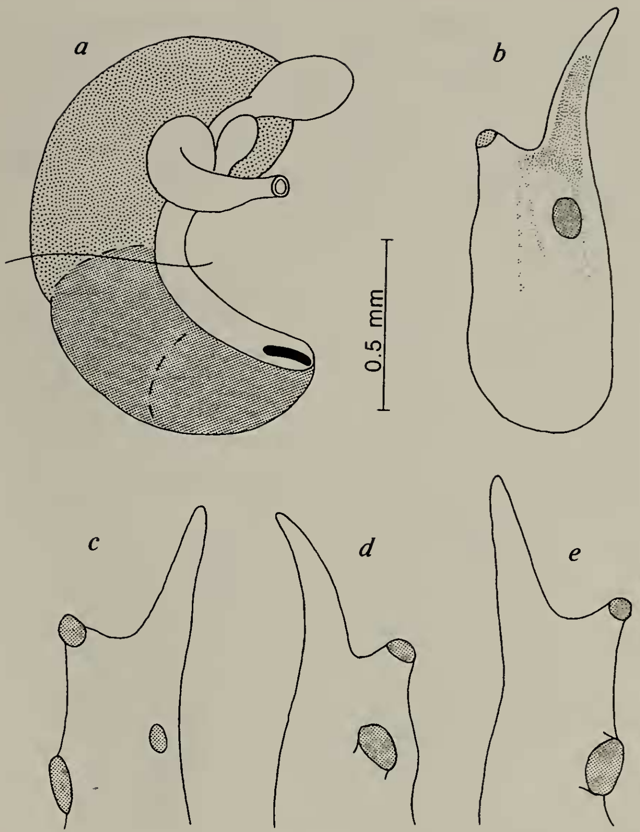

Fig. 39. Reproductive anatomy of *P.* cf. *stearnsiana,* USNM 857974, Sand Canyon: a, Left lateral view of pallial oviduct complex; b–e, Penes (b, c, dorsal aspects; d, e, ventral aspects).

Brown epithelial pigment dark on snout, dorsal tentacles, and all but narrow central strip of head/foot.

Radular (Fig. 62) formula: 5(6)–1–5(6)/2(3)–2(3), 3(4)–1–4(5), 19–26, 26–28 (from paratypes). Central tooth broadly trapezoidal, basal cusps small, basal process weakly excavated. Penis (Fig. 51e) longer than wide, moderately thickened. Distal tip with prominent swelling of inner side. Inner curvature with two small papillae positioned on inner curvature near tip, and larger basal papilla. Outer curvature with enlarged basal papilla. Dorsal penis variably pigmented by brown epithelial melanin, with especially dark cover on basal penis and papillae.

Type locality.—Spring brook in Cottonball Marsh, near base of Panamint Mountains at west side of salt pan in Death Valley, Inyo Co., California.

Distribution and habitat.—Found in a few small, cool, brackish (17°C, >5000 micromhos/cm) spring brooks emerging in

Fig. 40. Map showing distribution of *P.* cf. *stearnsiana* in the study area.

Cottonball Marsh, ca. 1.6 km out onto salt pan east of Salt Springs. Snails common on large, actively growing tufa blocks. Highly remote area in near-pristine condition.

Etymology.—Referring to highly mineralized spring habitat.

Remarks.—Very similar to *T. rowlandsi* from northern Death Valley, but distinguished by larger size, more highly developed shell sculpture, penial lobation pattern, and morphology of lateral radular teeth.

Tryonia variegata
Hershler and Sada, 1987
Amargosa tryonia
Figs. 51c, 52, 63, 64

Tryonia variegata Hershler & Sada 1987: 817.

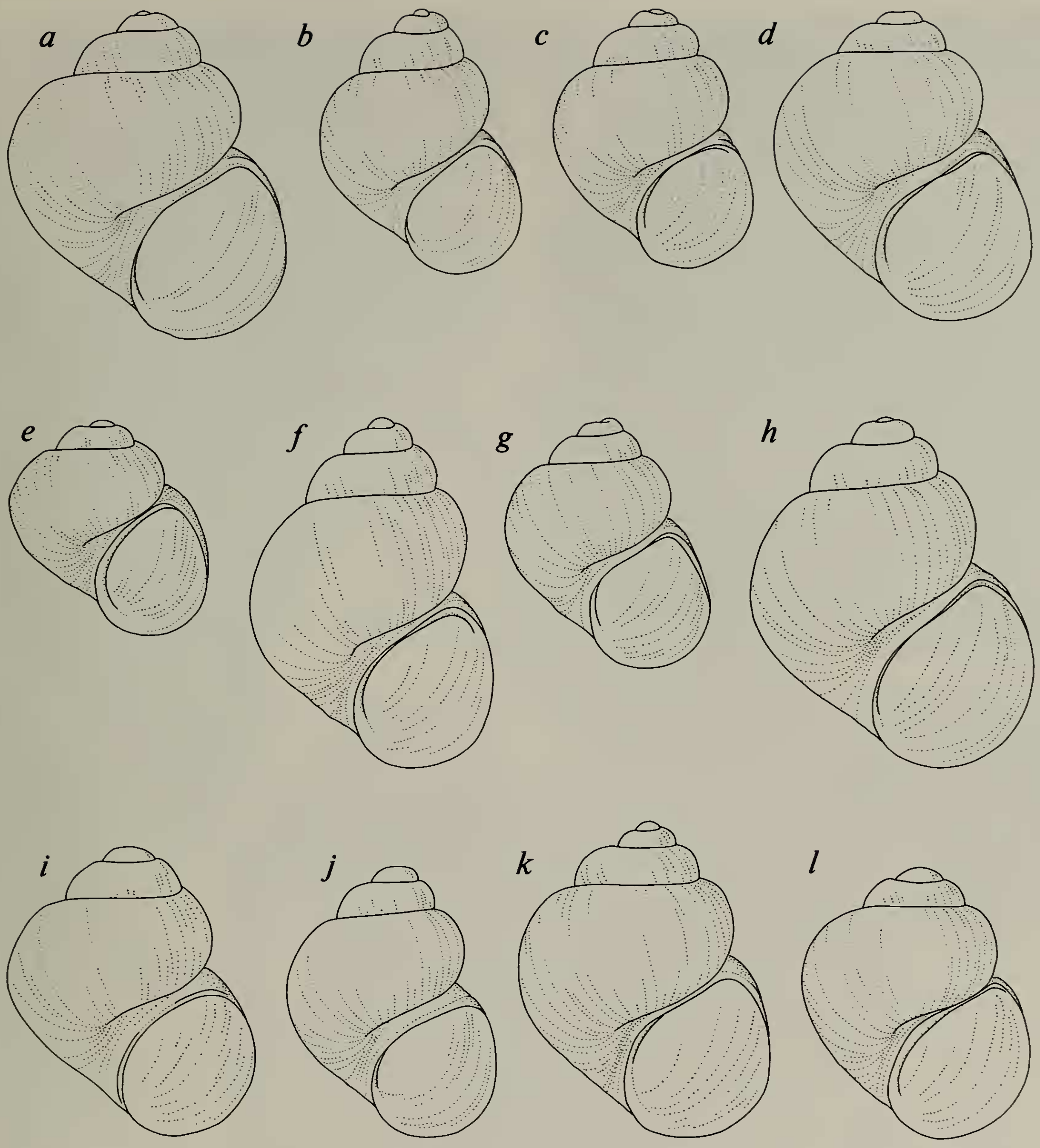

Fig. 41. Camera lucida drawings of shells of *P. wongi*: a, USNM 853531, spring alongside upper Pine Creek (2.18 mm); b, USNM 853524, spring N of Summit Creek (2.24 mm); c, USNM, 853527, Hogback Creek (Lone Pine) (1.74 mm); d, USNM 853530, spring S of Warren Lake (2.08 mm); e, USNM 853521, spring at Little Lake (1.44 mm); f, USNM 857947, French Spring (2.32 mm); g, USNM 857949, spring at Toll House (1.66 mm); h, USNM 857946, spring (north) at N end of Blind Spring Valley (2.34 mm); i, USNM 853536, Antelope Spring (1.90 mm); j, USNM 853535, Corral Springs (1.80 mm); k, USNM 853538, River Springs (2.66 mm); l, USNM 853537, Layton Spring (1.78 mm).

Material examined.—California: San Bernardino Co.; Saratoga Spring (204), USNM *853554, 27 Feb 1985; 857995, 10 Jul 1986. Inyo Co.; Spring crossing path on south side of Amargosa Gorge (208), 853553 (empty shell).—Spring in marsh east of Grimshaw Lake (209), *853551, 13 Mar 1985; 857994, 22 Mar 1987.—Shoshone Spring (211), *853550, 12 Mar 1985; 857993, 16 Mar 1987.—Resting Spring (212), 853552, 13 Mar 1985.

Diagnosis.—A variably-sized species with turriform-aciculate shell. Penis large, with 3 or 4 papillae on inner curvature and single

Fig. 42. SEM micrographs of *P. wongi* from west spring in Birchim Canyon: a, Holotype, USNM 860403 (2.14 mm); b, c, Paratypes, USNM 857941 (bar = 136 μm).

papilla (sometimes absent) on outer curvature.

Description.—Shell (Fig. 63) 1.2–7.5 mm high, height/width, 170–350%. Whorls, 4.75–9.75, slightly to moderately rounded, sometimes slightly shouldered. Sutures impressed. Body whorl 37–63% of shell height. Aperture narrowly ovate, apertural plane

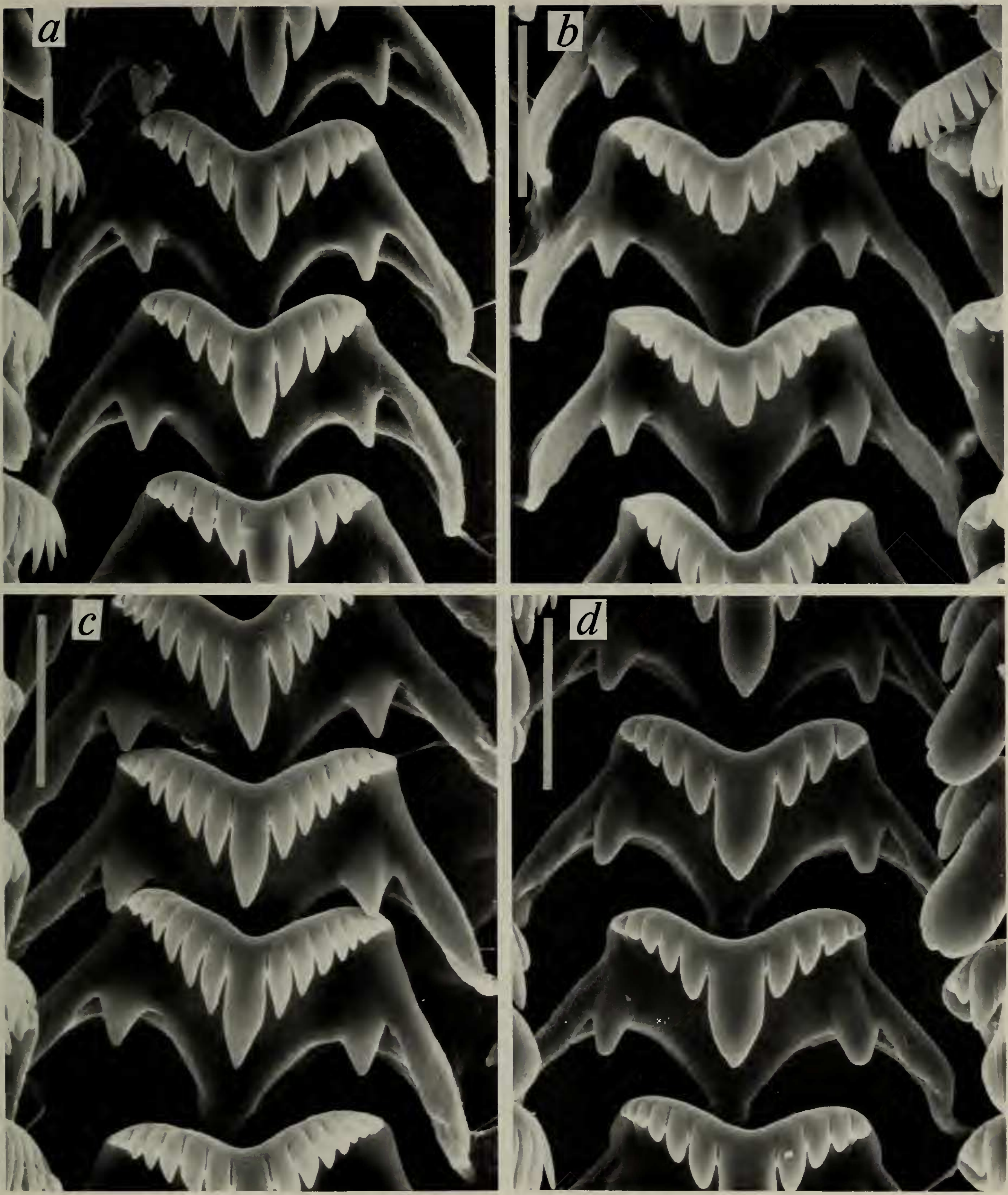

Fig. 43. Central radular teeth of *P. wongi*: a, USNM 857941, west spring in Birchim Canyon (bar = 10 μm); b, USNM 853521, spring at Little Lake (bar = 7.5 μm); c, USNM 853536, Antelope Spring (bar = 7.5 μm); d, USNM 857981, River Springs (bar = 12 μm).

near-parallel with coiling axis. Inner lip slightly thickened and reflected, adnate to or slightly separated from body whorl. Outer lip thin, slightly to moderately sinuate. Umbilicus chink-like to moderately open. Protoconch smooth to irregularly wrinkled (Fig. 63d). Growth lines often highly pronounced.

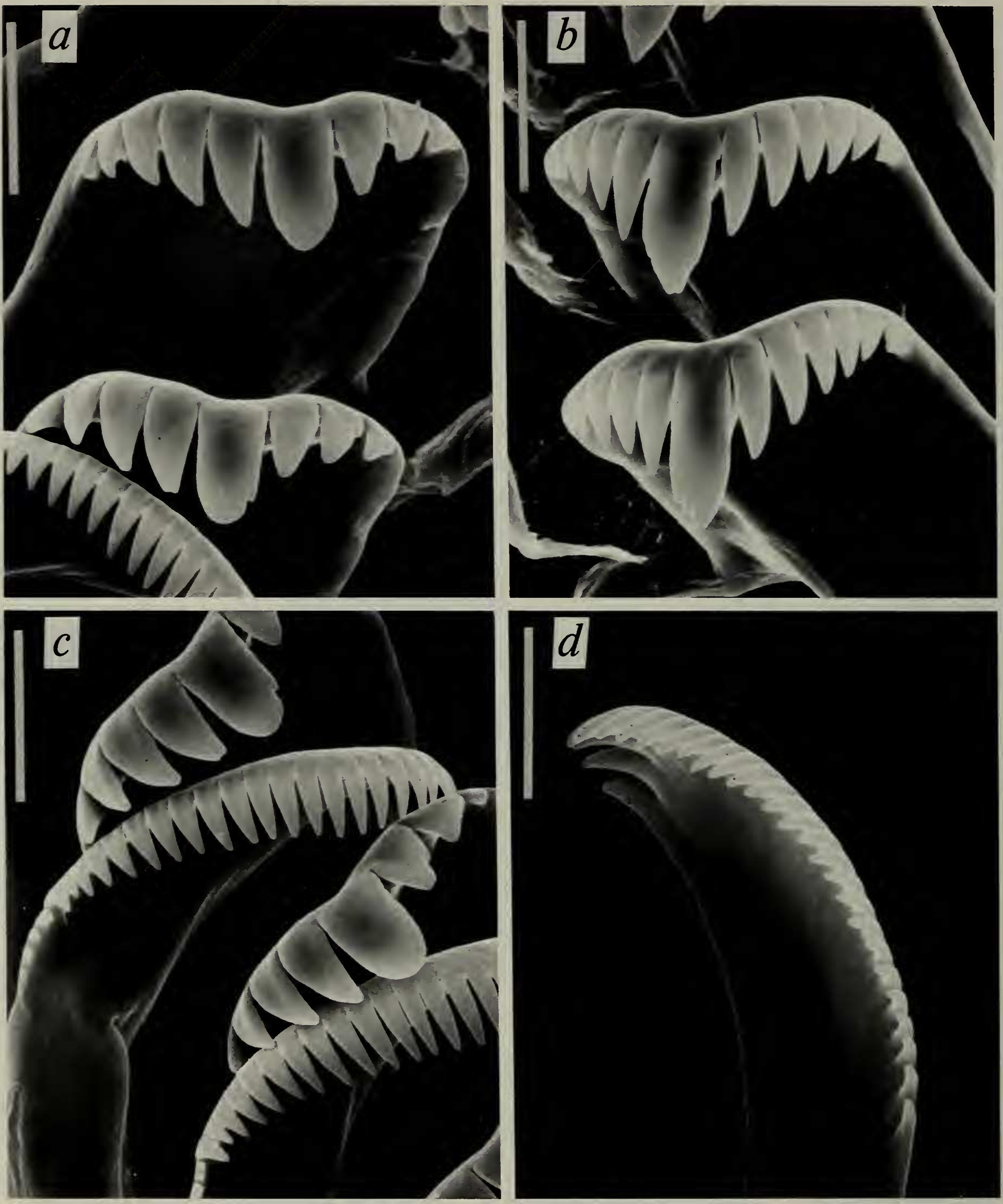

Fig. 44. Lateral and marginal teeth of *P. wongi*: a (laterals), c (laterals and inner marginals), d (outer marginals), USNM 857941, west spring in Birchim Canyon (bars = 6.0 μm); b, Laterals, USNM 853536, Antelope Spring (bar = 6.0 μm).

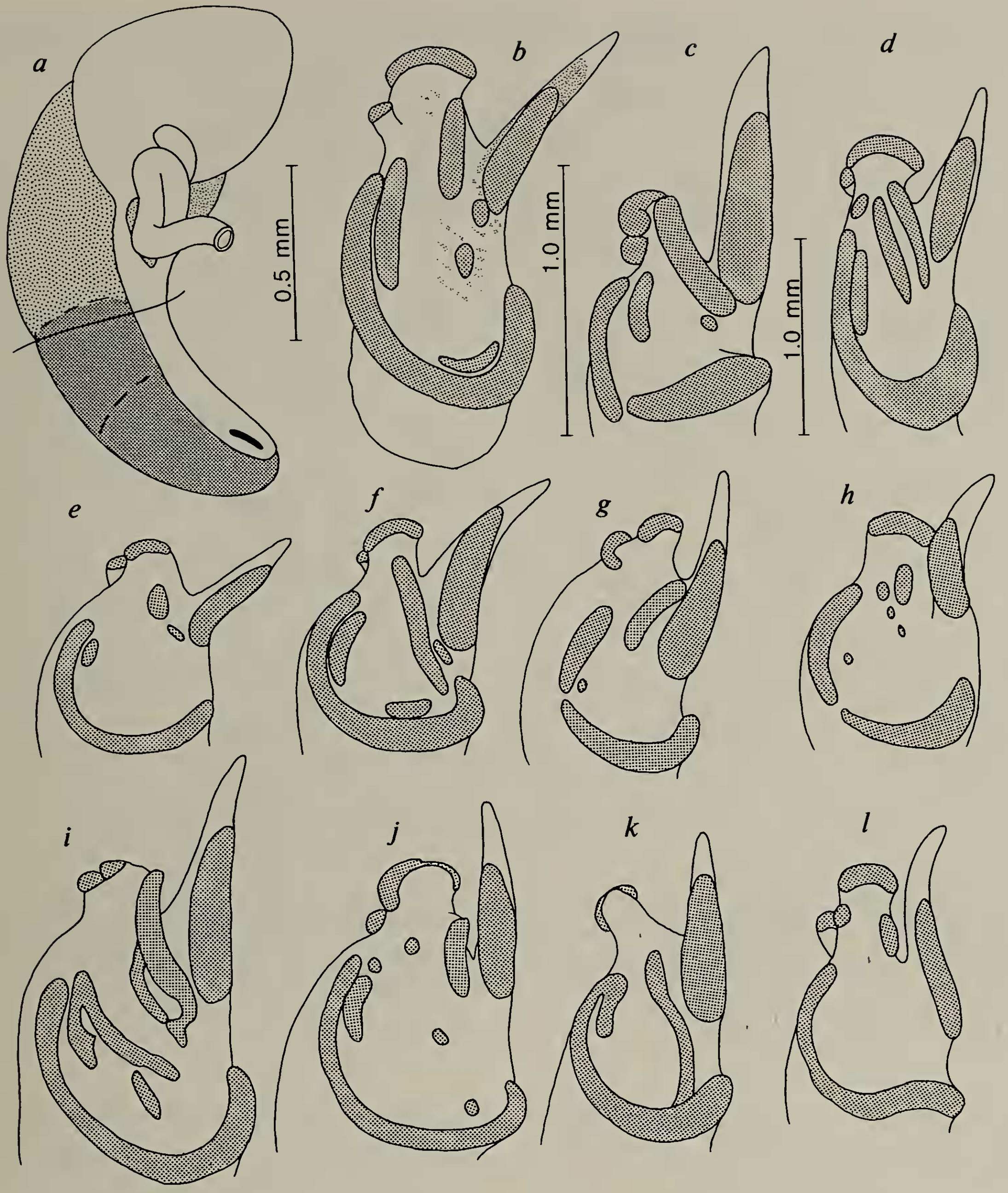

Fig. 45. Reproductive anatomy of *P. wongi*: a, Left lateral view of pallial oviduct complex, USNM 857941, west spring in Birchim Canyon; b–l, Dorsal penes (b, USNM 857941, west spring in Birchim Canyon; c, USNM 853530, spring S of Warren Lake; d, USNM 857981, River Springs; e, USNM 857979, Corral Springs; f, USNM 857980, Layton Spring; g, USNM 857947, French Spring; h, USNM 857949, spring at Toll House; i, USNM 853534, spring (north) at northern end of Blind Spring Valley; j, USNM 857978, spring in Owens Gorge; k, USNM 857942, spring alongside Lubkin Creek; l, USNM 853523, Summit Creek). "c"–"l" drawn to same scale.

Radular (Fig. 64) formula: (4–7)–1–(4–7)/2(3)–2(3), 3(4)–1–4(5), 17–30, 22–33 (from numerous populations). Central tooth typically broadly trapezoidal; basal cusps moderate to large-sized, basal process moderately excavated.

Epithelial pigment usually dark brown-black on snout and sides of head/foot, with lighter cover on central portions of latter.

Type locality.—Five Springs, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Amargosa River drainage, from Ash Meadows south to Saratoga Spring. Snails typically common

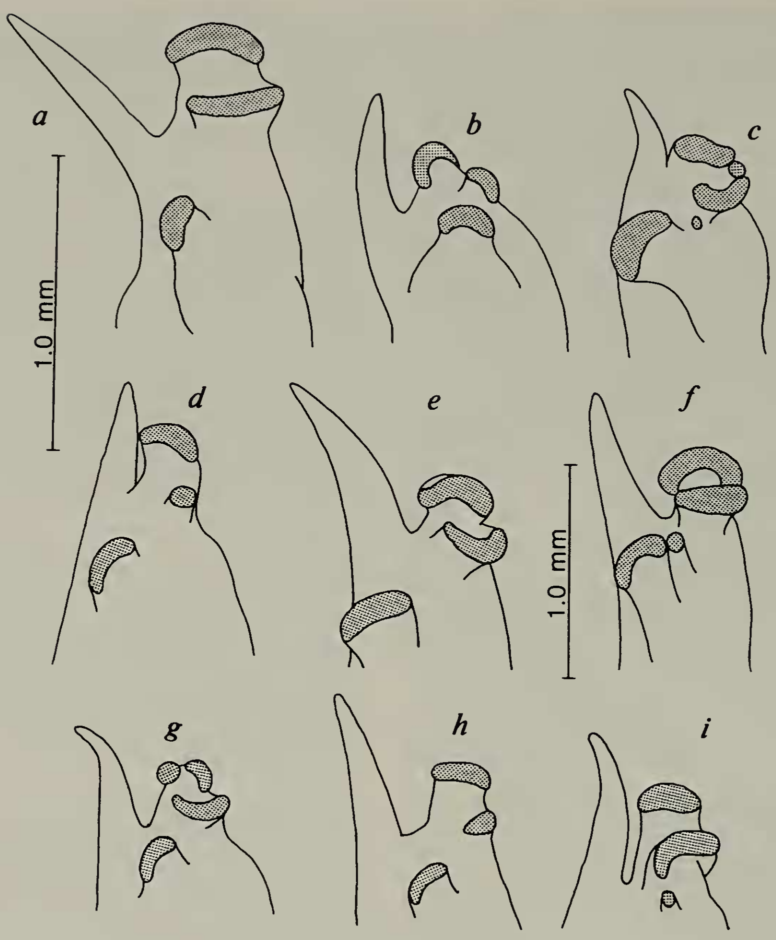

Fig. 46. Penes (ventral aspects) of *P. wongi*: a, USNM 857941, west spring in Birchim Canyon; b, USNM 857947, French Spring; c, USNM 853536, Antelope Spring; d, USNM 857942, spring alongside Lublin Creek; e, USNM 853534, spring (north) at northern end of Blind Spring Valley; f, USNM 857981, River Springs; g, USNM 857949, spring at Toll House; h, USNM 857979, Corral Spring; i, USNM 853523, Summit Creek. "a"–"e" and "g"–"i" drawn to same scale.

on various substrates in small springpools and upper portions of outflows (7–32°C, 430–10,150 micromhos/cm).

Remarks.—Populations from lower Amargosa River drainage are clearly assignable to *T. variegata* on basis of shell, radular, and penial features.

Morphometrics

Discriminant analyses were performed on each of three groups of congeners from given portions of the study area: a) *P. amargosae* and *P. micrococcus,* very similar forms with contiguous ranges; b) *Pyrgulopsis* fauna of Owens Valley (*P. aardahli, P. owensensis, P. perturbata, P.* cf. *stearnsiana, P. wongi*); and c) small-sized *Tryonia* spp., including those of northern Death Valley (*T. salina, T. rowlandsi, T. margae*) and Ash Meadows (*T. ericae, T. elata*).

Results (summarized in Tables 3–5) support taxonomy presented herein, insofar as high correct classifications (81–87% [overall]) indicate that these snails are well-differentiated in shell features. In the analysis involving *P. amargosae* and *P. micrococcus,* correct classification was 89% (40/45) and 80% (291/362) for each species, respectively. Correct classification for two populations of *P. amargosae* (Amargosa Gorge, Grimshaw Lake) from Tecopa area (where the ranges abut) was high (83%), as was that (92%) for two nearby populations of *P. mi-*

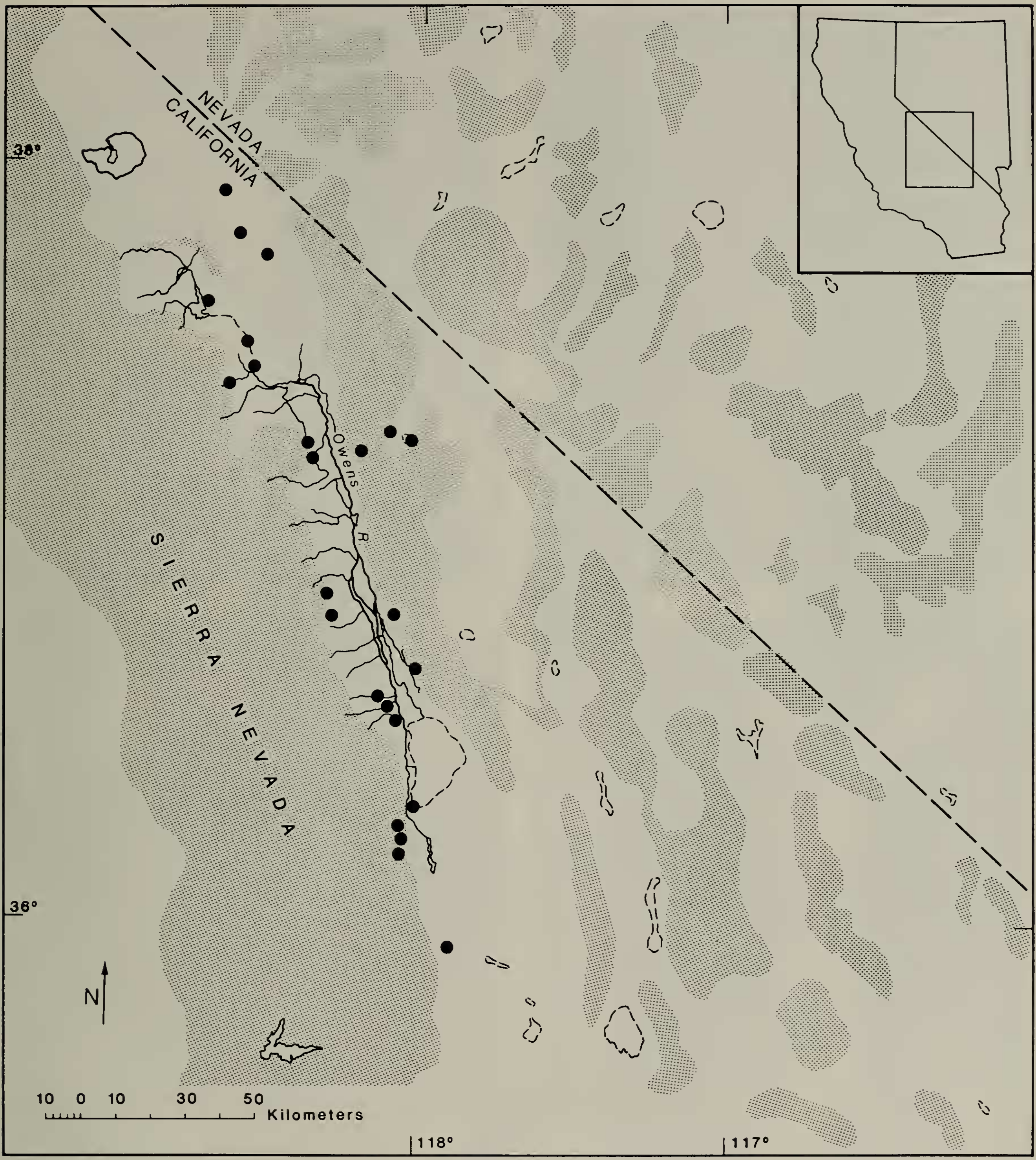

Fig. 47. Map showing distribution of *P. wongi.*

crococcus (Tecopa Hot Springs, Shoshone Spring). Misclassified specimens of *P. micrococcus* were concentrated in a few populations in northern Death, Panamint, and Saline Valleys (well separated from the range of *P. amargosae*), and indicate local differentiation of this relatively widespread form. In this analysis, discrimination was based largely on height of shell and aperture.

For the Owens Valley *Pyrgulopsis,* correct classification was 84% overall (382/451), and ranged from 79–87% by species. The sole species having <80% correct classification, *P. owensensis,* was most frequently

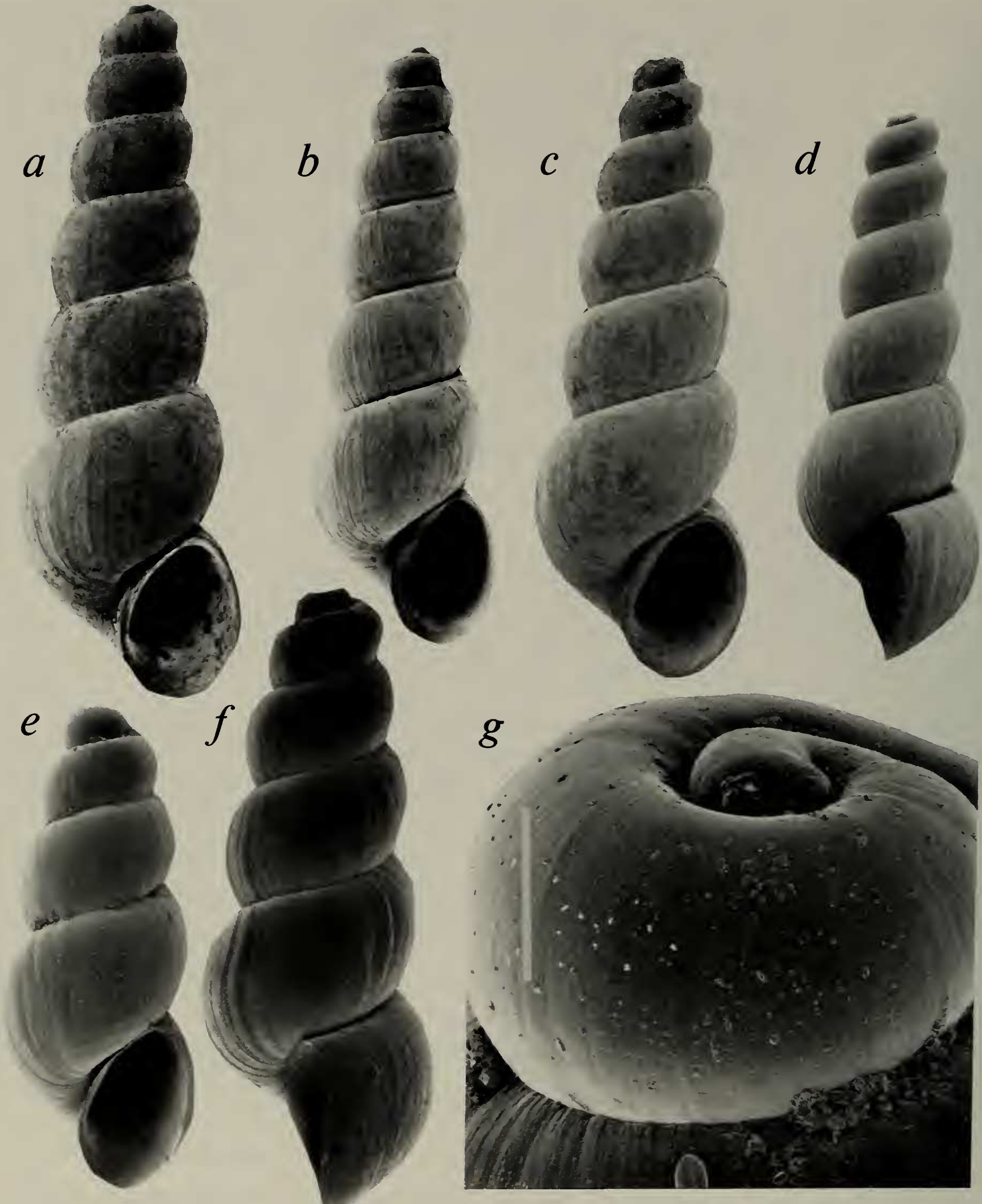

Fig. 48. SEM micrographs of *T. margae*: a–d, Grapevine Springs, upper warm spring (a, holotype, USNM 860408, [3.52 mm]; b–d, Paratypes, USNM 857952); e–g, USNM 853555, Grapevine Springs, spring above shack (bar = 86 μm).

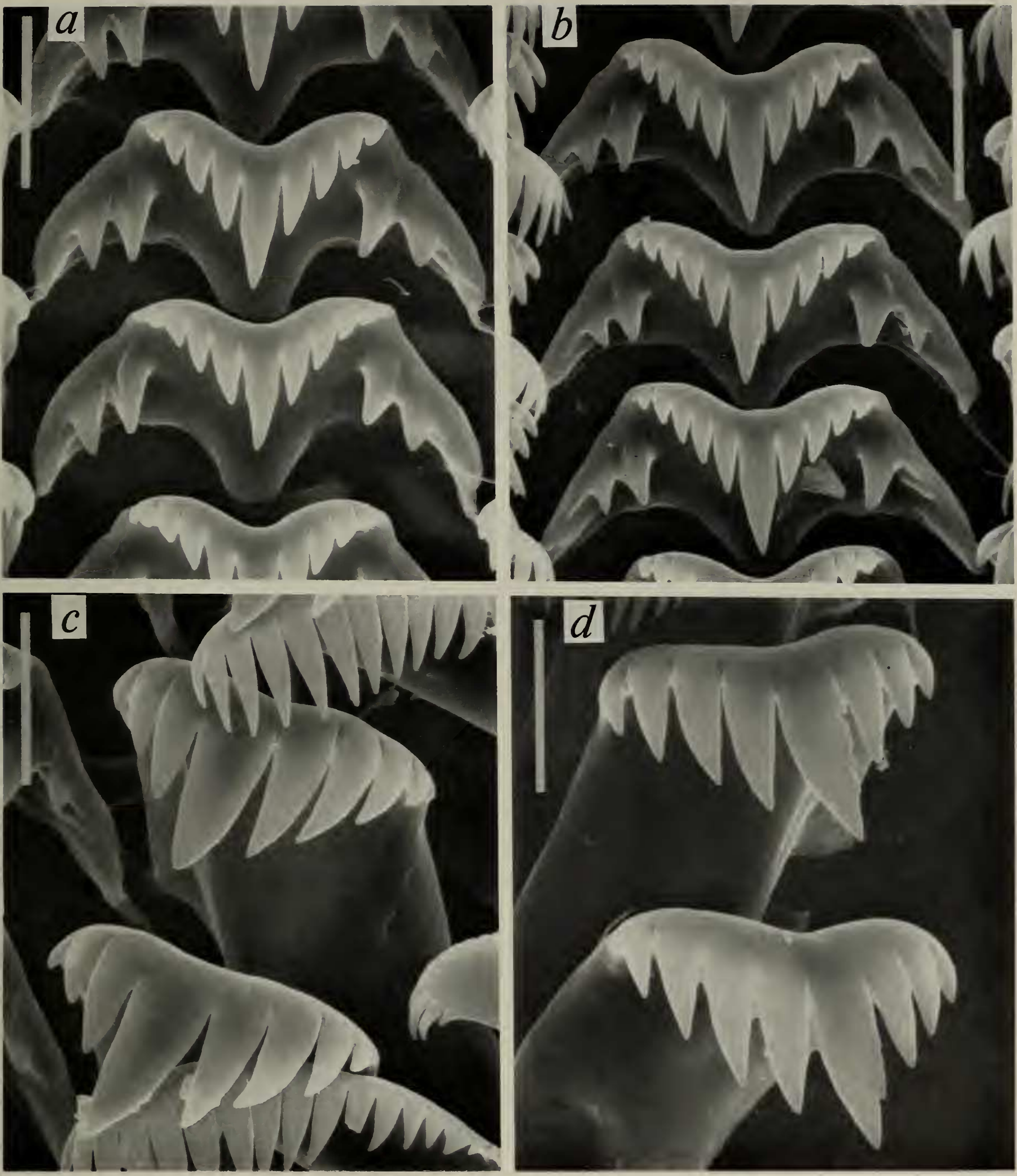

Fig. 49. Central and lateral radular teeth of *T. margae*: a, c, USNM 857953, Grapevine Springs, upper warm spring (a, centrals, bar = 6.7 μm; c, laterals and inner marginals, bar = 6.7 μm); b, d, USNM 857996, Grapevine Springs, spring above shack (b, centrals, bar = 6.7 μm; d, laterals, bar = 6.7 μm).

(10/14) misclassified as *P. wongi,* which cannot be confused with the former when penial morphology is considered. Parameters weighing heavily on the first discriminant function were related to size and width of shell and aperture.

Classification of each of the three small-sized *Tryonia* spp. from northern Death

Fig. 50. Marginal radular teeth of *T. margae*: a, c, USNM 857953, Grapevine Springs, upper warm spring (a, laterals and inner marginals, bar = 10.0 μm; c, outer marginal, bar = 3.8 μm); b, d, USNM 857996, Grapevine Springs, spring above shack (b, laterals and inner marginals, bar = 7.5 μm; d, outer marginal, bar = 3.8 μm).

Valley was 100%, while that of *T. elata* and *T. ericae* from Ash Meadows was 93% and 95%, respectively. Despite their general similarity in form, *T. margae* and *T. elata* were well-discriminated, with only a single specimen (of the latter) misclassified (as the former). Parameters weighing heavily on the first discriminant function were shell height,

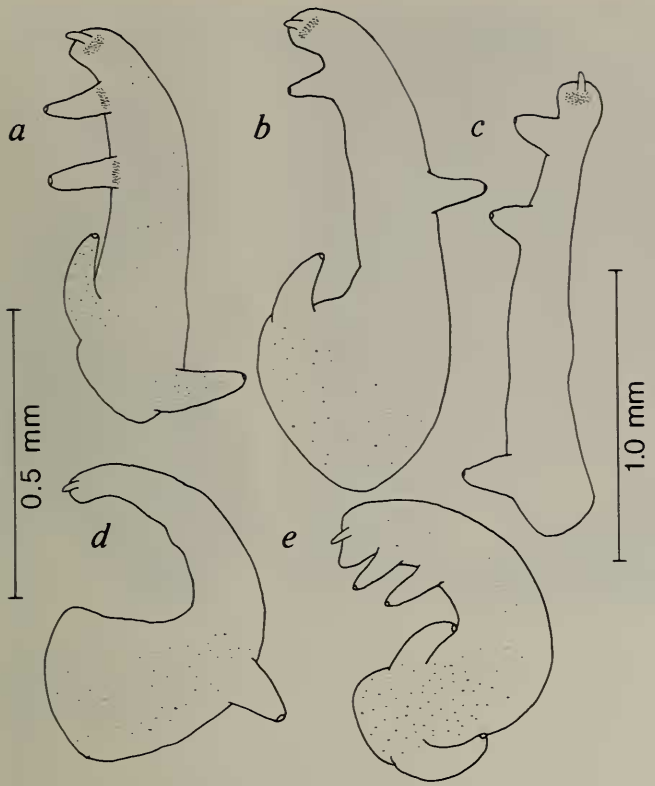

Fig. 51. Penes (dorsal aspects) of *Tryonia* spp.: a, *T. margae,* USNM 857952, Grapevine Springs, upper warm spring; b, *T. rowlandsi,* USNM 857953, Grapevine Springs, upper warm spring; c, *T. variegata,* USNM 857994, spring at Grimshaw Lake; d, *T. robusta,* USNM 857999, Nevares Springs, upper spring; e, *T. salina,* USNM 857998, Cottonball Marsh. "a," "b," "d," "e" drawn to same scale.

width of body whorl, and aperture size and shape.

Discussion

Modern drainage in the Death Valley area includes Owens, Amargosa, and Mojave Rivers, the latter two of which are dry along most of their courses. Although now isolated from one another, these river systems were integrated during wetter, pluvial times during the Pleistocene as a series of lakes overflowed along their courses to terminate in Death Valley. This Death Valley System (named by Miller 1943:69) was initially proposed by Gale (1914) and Blackwelder (1933), and has been discussed in detail by many others (Hubbs & Miller 1948; Miller 1946, 1948; Smith 1978; Soltz & Naiman 1978; Smith & Street-Perrott 1983; Minckley et al. 1986; Taylor 1986). Configuration of the System is portrayed in Fig. 65 as prelude to discussion of springsnail zoogeography.

Table 3.—Results of discriminant function analysis on *Pyrgulopsis amargosae* and *P. micrococcus.* Also given are the canonical correlation, number of specimens used (by species, ordered as above), and percent correct classification (overall).

Variables	Standardized coefficients	Correlations
WH	0.365	0.554
SH	1.194	0.354
SW	0.398	−0.094
LBW	−0.717	0.176
WBW	0.749	0.146
AL	−1.728	0.055
AW	−0.067	−0.108
W	0.176	−0.292
D	0.798	0.536
T	−0.390	0.425
SA	0.871	0.351
C. correlation	0.475	
N	45,362	
% correct classification	81	

Springsnail distributions reflect pronounced local endemism of the modern fauna. Twenty of 22 species known from Death Valley System area are restricted to its confines. Of these, 10 are endemic to single springs or spring complexes, and another seven occur in relatively small portions of single modern drainage basins. Locally endemic *Pyrgulopsis* are concentrated in Owens Valley and Ash Meadows, while endemic *Tryonia* occur in the latter and northern Death Valley. Three forms are relatively widespread in the system: *P. wongi,* of pluvial Owens River drainage (Long, Adobe, Owens Valleys); *P. micrococcus,* widely distributed from Amargosa Valley west to Panamint Valley; and *T. variegata,* of pluvial Amargosa River drainage (Ash Meadows, Tecopa Basin, Saratoga Spring [southern Death Valley]).

Endemic *Pyrgulopsis* of Owens Valley and

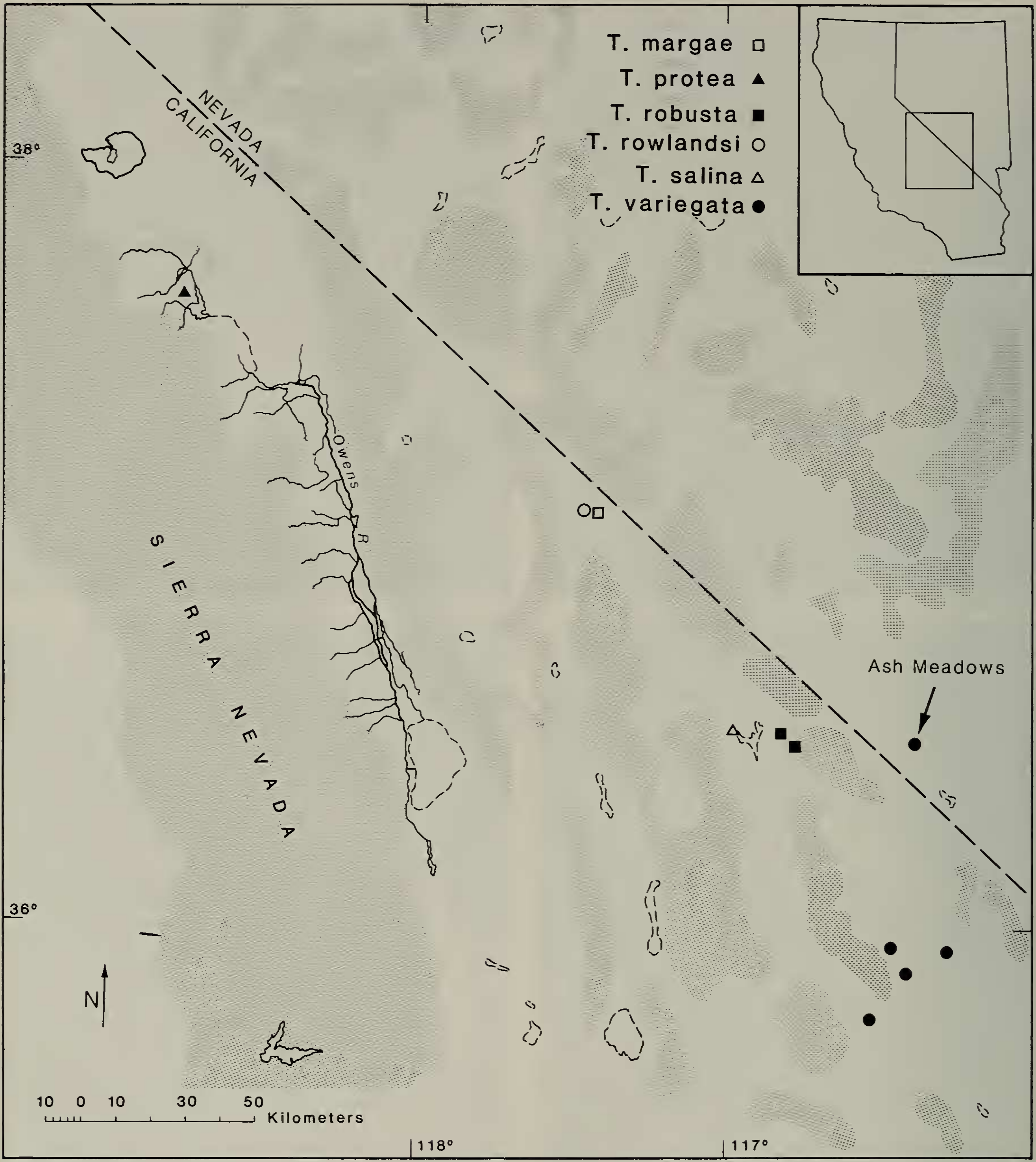

Fig. 52. Map showing distribution of *Tryonia* spp. in study area. *Tyronia variegata* occurs at 18 localities in Ash Meadows.

Amargosa Basin are sharply differentiated on basis of penial morphology and represent separate local radiations. Owens Valley forms, characterized in part by possession of a ventral penial swelling bearing glandular ridge (absent in forms endemic to Amargosa drainage), include a group comprising *P.* cf. *stearnsiana* and similar, endemic forms (*P. aardahli, P. owensensis, P. perturbata*); and *P. wongi,* which has no close relatives in the study area. Ash Meadows (Amargosa Basin) endemics represent at

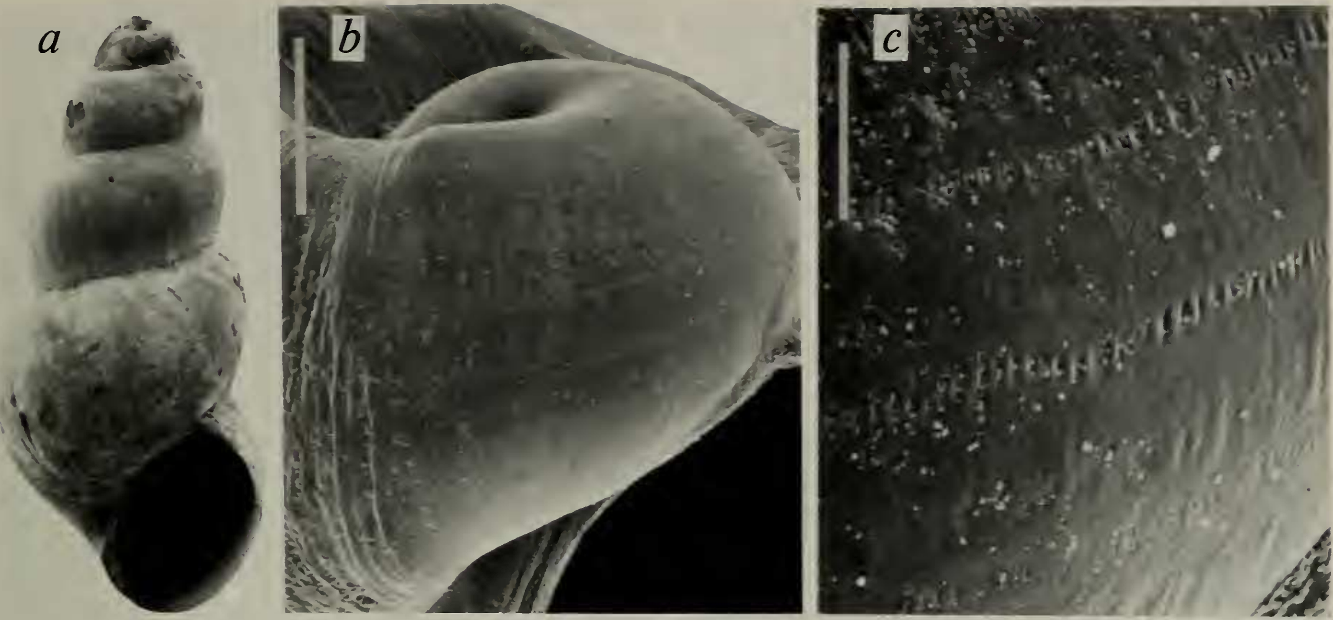

Fig. 53. SEM micrographs of *T. protea*, USNM 857954, Hot Creek. Shell "a" is 3.64 mm tall. "b," "c" show sculpture on protoconch of embryonic shell (bars = 60, 17.6 μm).

least two lineages (both including *Fluminicola*-like representatives): snails with reduced or absent penial lobes and a glandular ridge on mid-ventral penial surface (*P. erythropoma, P. crystalis, P. pisteri*); and those having a ridge on terminal portion of moderate-large sized penial lobes (*P. fairbanksensis, P. nanus, P. isolatus*). The latter may be related to the probable sister species pair of widespread *P. micrococcus* and *P. amargosae* from southern Amargosa River drainage.

Relationships among regional *Tryonia* are more speculative. Endemic *Tryonia* in

Table 4.—Results of discriminant function analysis on Owens Valley *Pyrgulopsis* (*P. aardahli, P. owensensis, P. perturbata, P.* cf. *stearnsiana, P. wongi*). Also given are canonical correlations, number of specimens used (by species, ordered as above), and percent correct classification (overall).

	Standardized coefficients		Correlations	
Variable	Function 1	Function 2	Function 1	Function 2
WH	0.580	−0.841	−0.277	−0.711
SH	−2.972	0.489	−0.708	−0.534
SW	1.037	2.483	−0.549	−0.466
LBW	0.513	−2.301	−0.641	−0.527
WBW	1.367	−2.253	−0.558	−0.555
AL	2.937	−0.550	−0.553	−0.424
AW	−3.827	1.822	−0.617	−0.387
W	0.075	−0.317	0.255	−0.068
D	0.285	0.453	−0.105	−0.120
T	−0.143	0.904	−0.397	−0.042
SA	−0.810	0.600	0.085	−0.164
C. correlation	0.771	0.687		
N	15, 86, 39, 25, 286			
% correct classification	84			

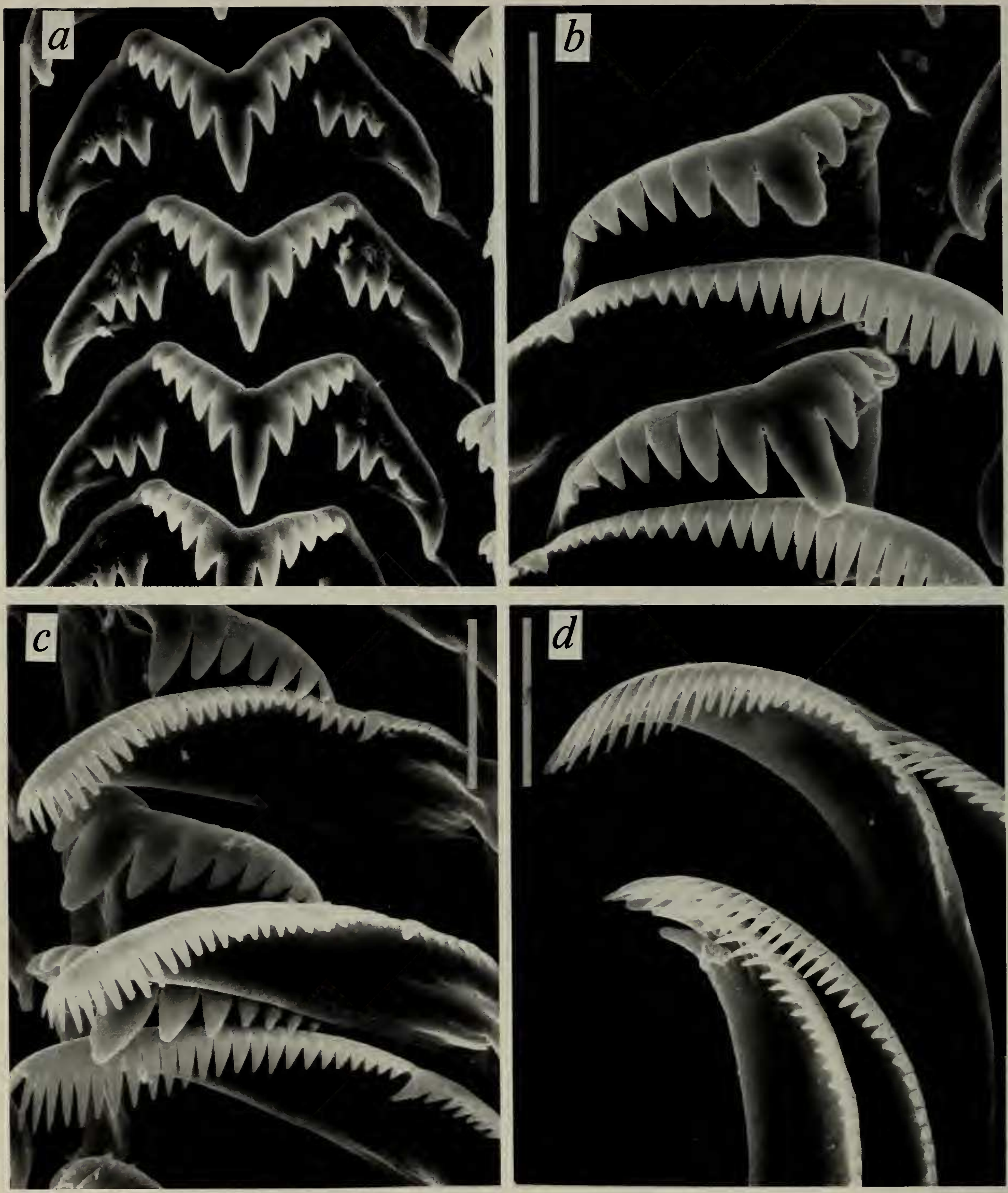

Fig. 54. Radula of *T. protea,* USNM 857954, Hot Creek: a, Centrals (bar = 12 μm); b, c, Laterals and inner marginals (bars = 8.6 μm); d, Outer marginals (bar = 7.5 μm).

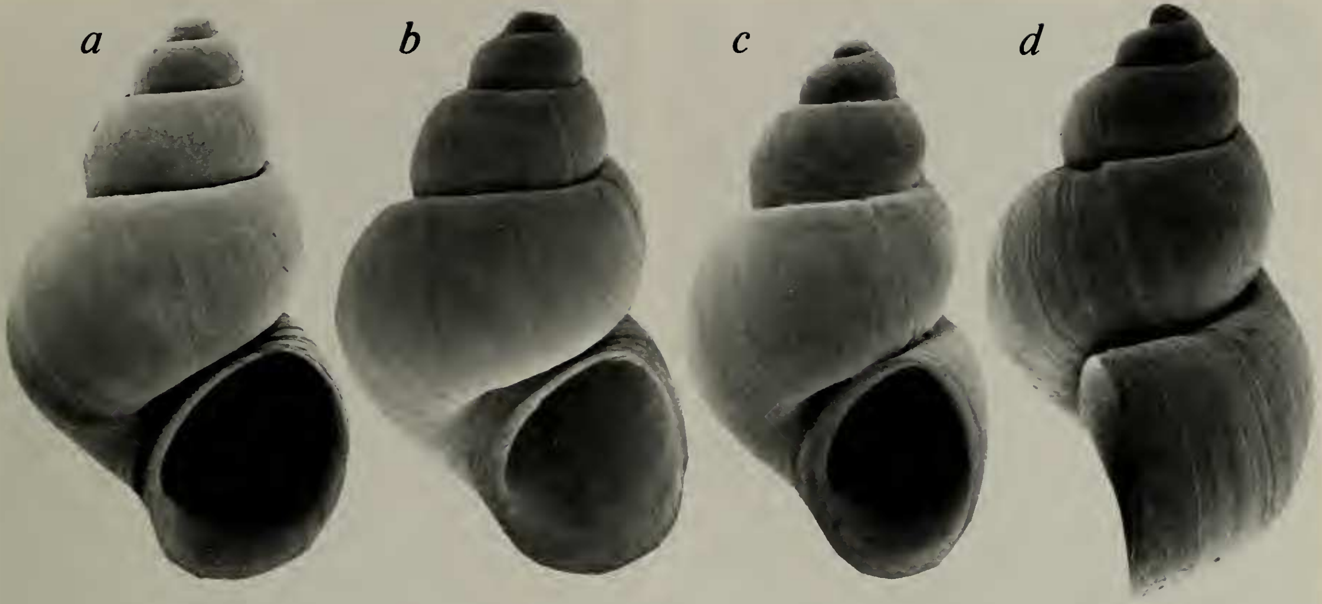

Fig. 55. SEM micrographs of *T. robusta* from Nevares Springs, upper spring: a, Holotype, USNM 860411 (1.92 mm); b–d, Paratypes, USNM 853557.

northern Death Valley and Ash Meadows, apart from enigmatic *T. robusta,* apparently comprise a single local radiation. *T. protea* from west of Death Valley (Long and [fossil; Taylor 1985:317] Panamint Valleys) is quite similar (in shell) to at least one representative from the east, *T. variegata* (contrary to Taylor 1985:317) and may not represent a separate lineage (as implied by Taylor 1985:317).

Pluvial waters of the Death Valley System provided aquatic continuity (and thus the

Table 5.—Results of discriminant function analysis on small-sized *Tryonia* (*T. elata, T. ericae, T. margae, T. rowlandsi, T. salina*). Also given are canonical correlations, number of specimens used (by species, ordered as above), and percent correct classification (overall).

Variable	Standardized coefficients		Correlations	
	Function 1	Function 2	Function 1	Function 2
WH	−0.044	0.672	0.109	0.487
SH	1.592	0.600	−0.178	0.699
SW	0.393	0.735	−0.580	0.432
LBW	0.423	−0.227	−0.402	0.535
WBW	−1.357	−0.908	−0.521	0.493
AL	−1.813	−0.341	−0.510	0.580
AW	0.003	0.634	−0.622	0.405
W	−0.031	0.081	−0.077	−0.312
D	0.286	0.191	0.032	−0.030
T	−0.071	0.429	0.131	0.427
SA	0.736	0.828	0.073	0.353
C. correlation	0.994	0.975		
N	30, 19, 6, 16, 15			
% correct classification	97			

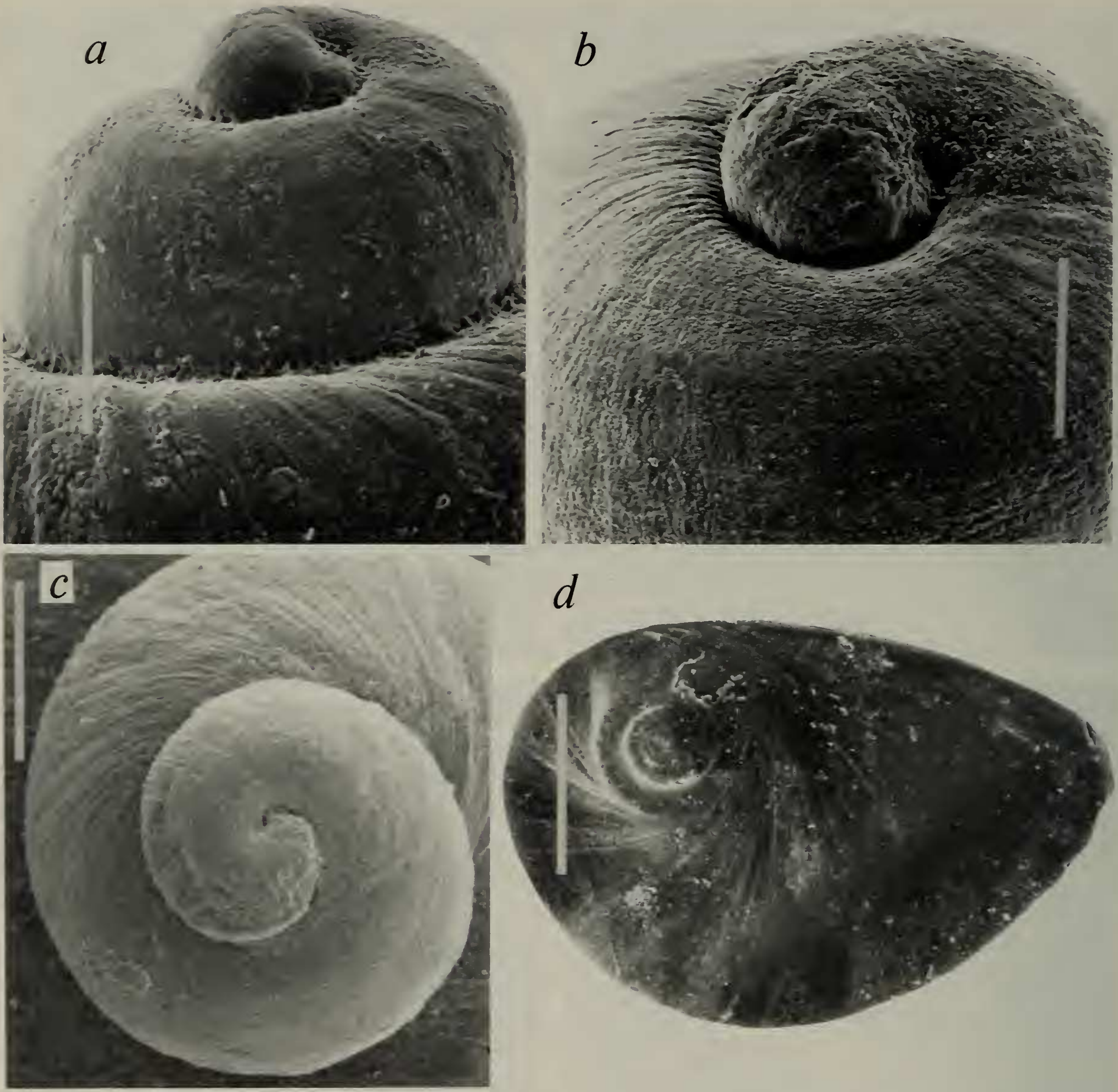

Fig. 56. SEM micrographs of *T. robusta,* Nevares Springs, upper spring, USNM 853557: a–c, Views of apex (bars = 75, 43, 100 μm); d, Dorsal operculum (bar = 200 μm).

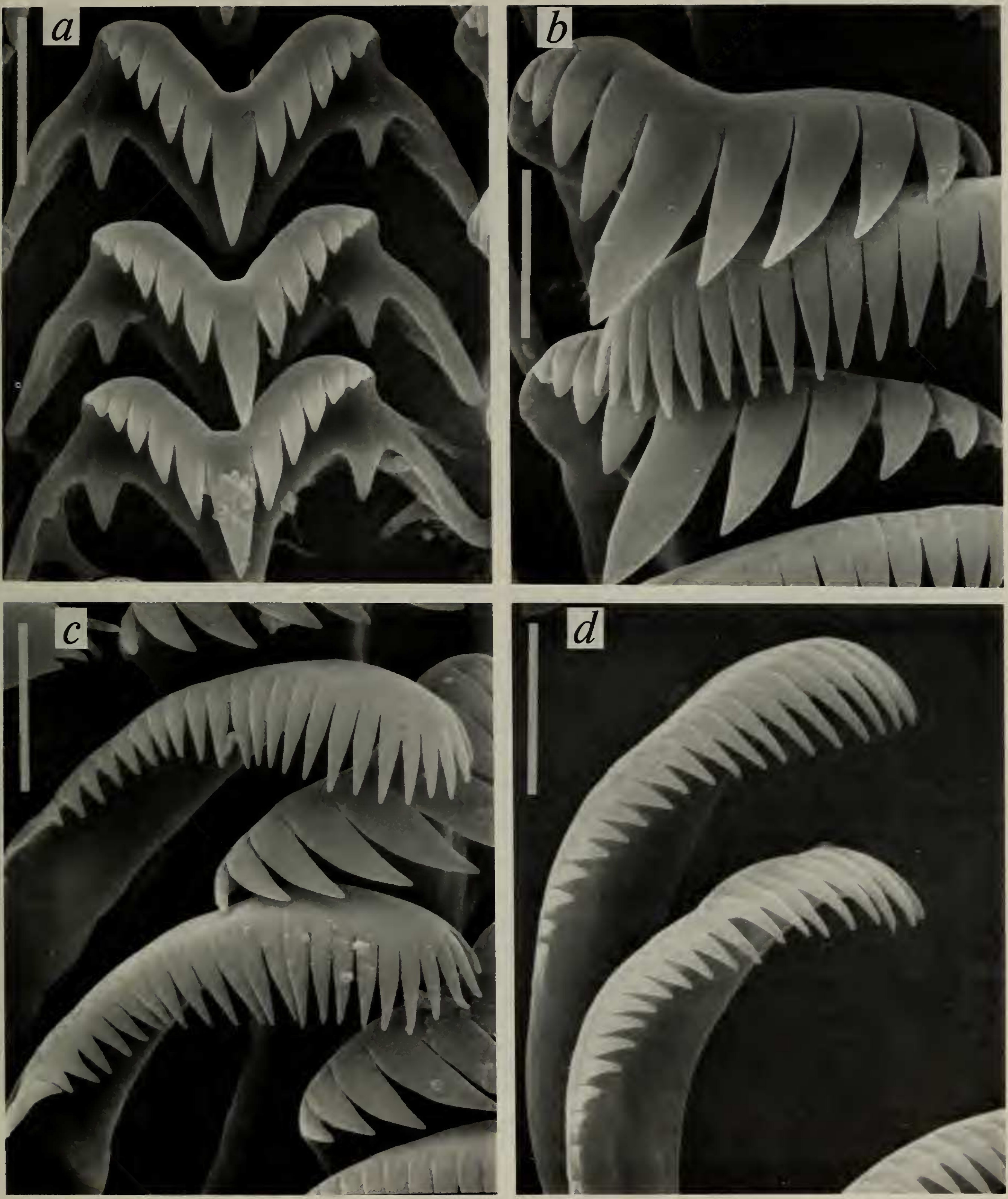

Fig. 57. Radula of *T. robusta,* Nevares Springs, upper spring, USNM 857999: a, Centrals (bar = 6.0 μm); b, c, Laterals and inner marginals (bars = 3.8, 5.0 μm); d, Outer marginals (bar = 3.8 μm).

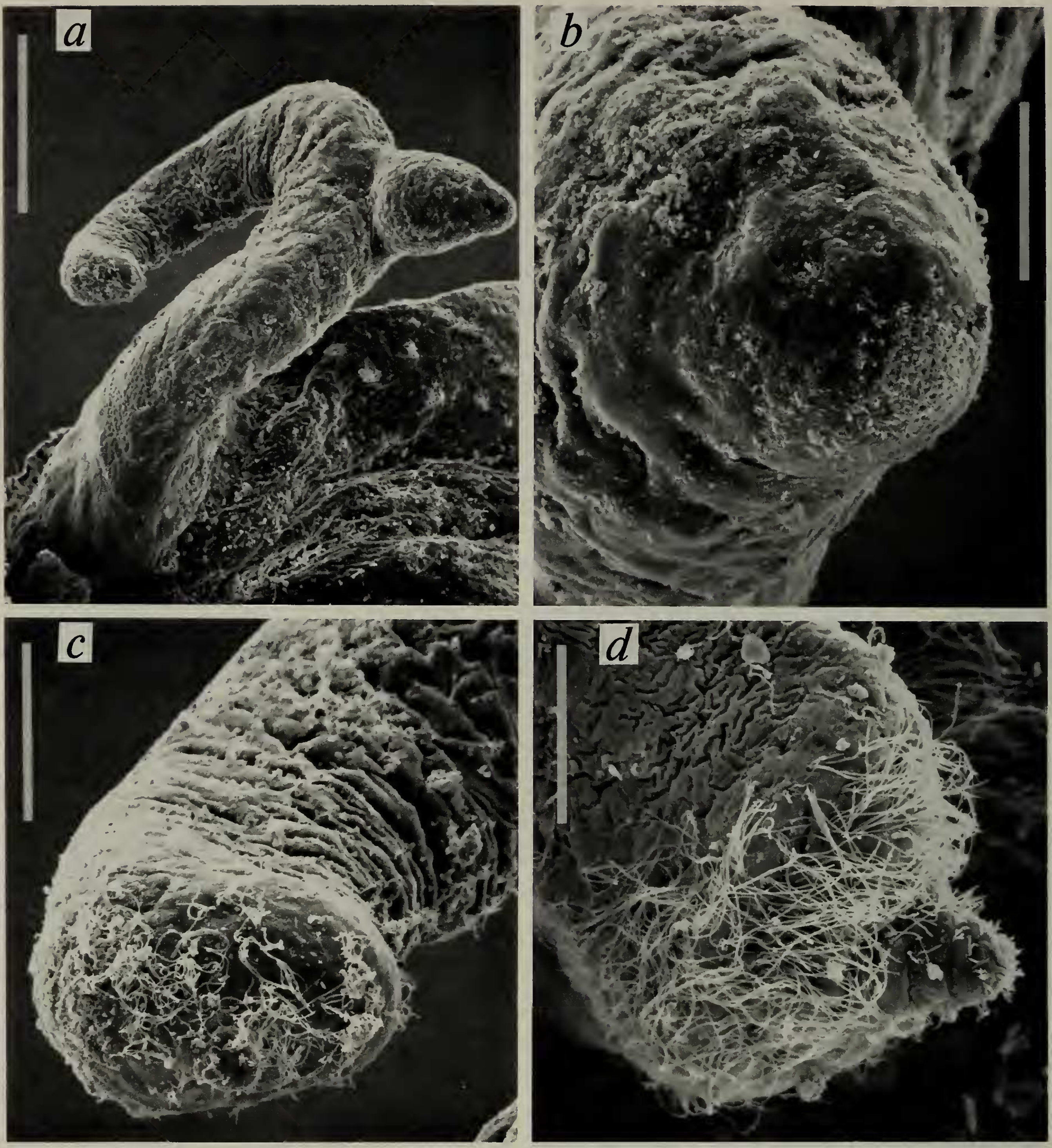

Fig. 58. SEM micrographs of penes of *T. robusta,* USNM 857999, Nevares Springs, upper spring: a, Dorso-right lateral aspect, with attachment to head on lower left (bar = 136 μm); b, Distal tip of papilla (bar = 23.1 μm); c, d, Distal tips of penis, showing ciliation (bars = 30, 20 μm).

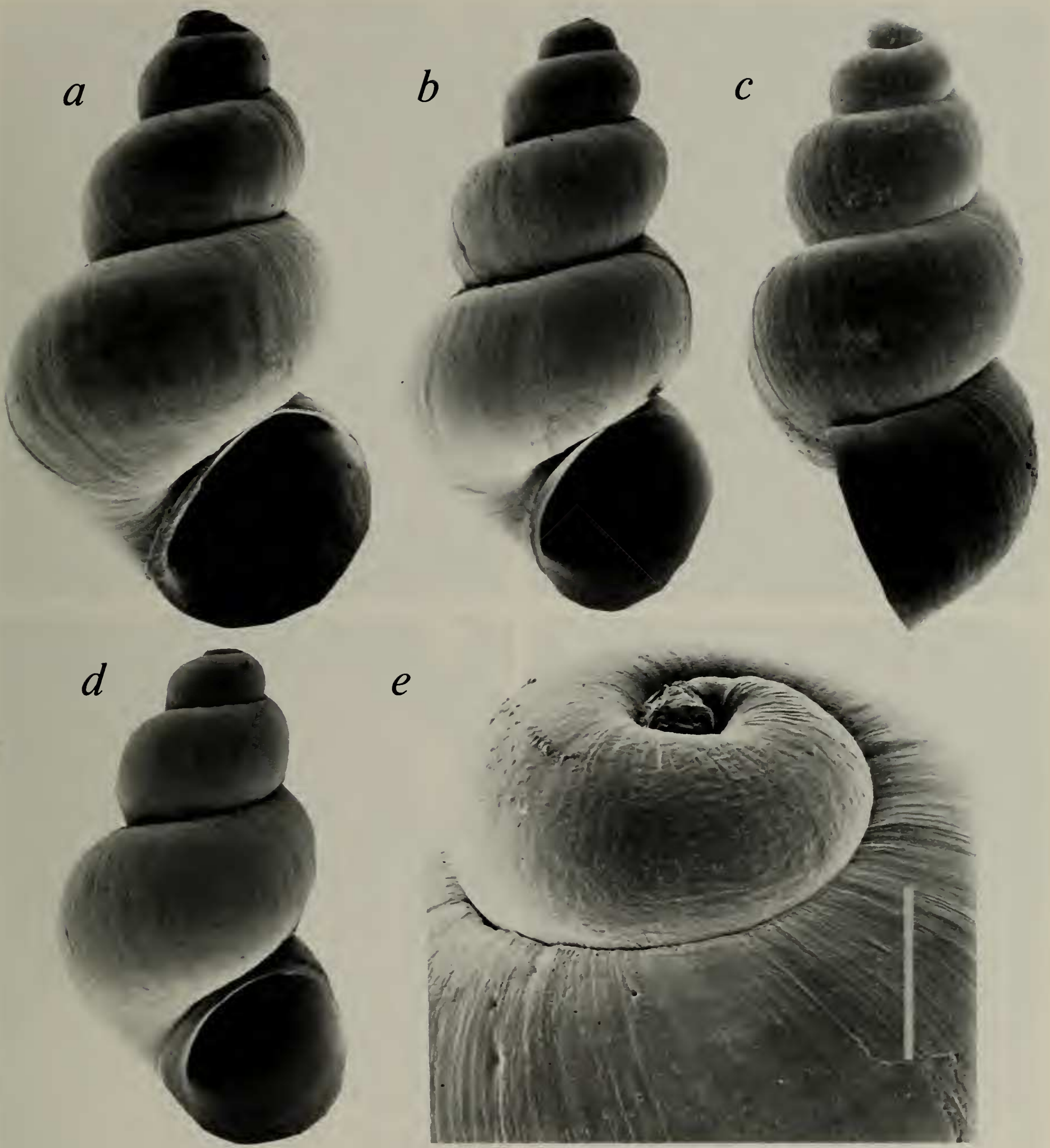

Fig. 59. SEM micrographs of *T. rowlandsi* from Grapevine Springs, upper warm spring: a, Holotype, USNM 860409 (2.18 mm); b–e, Paratypes, USNM 857953 (bar = 100 μm).

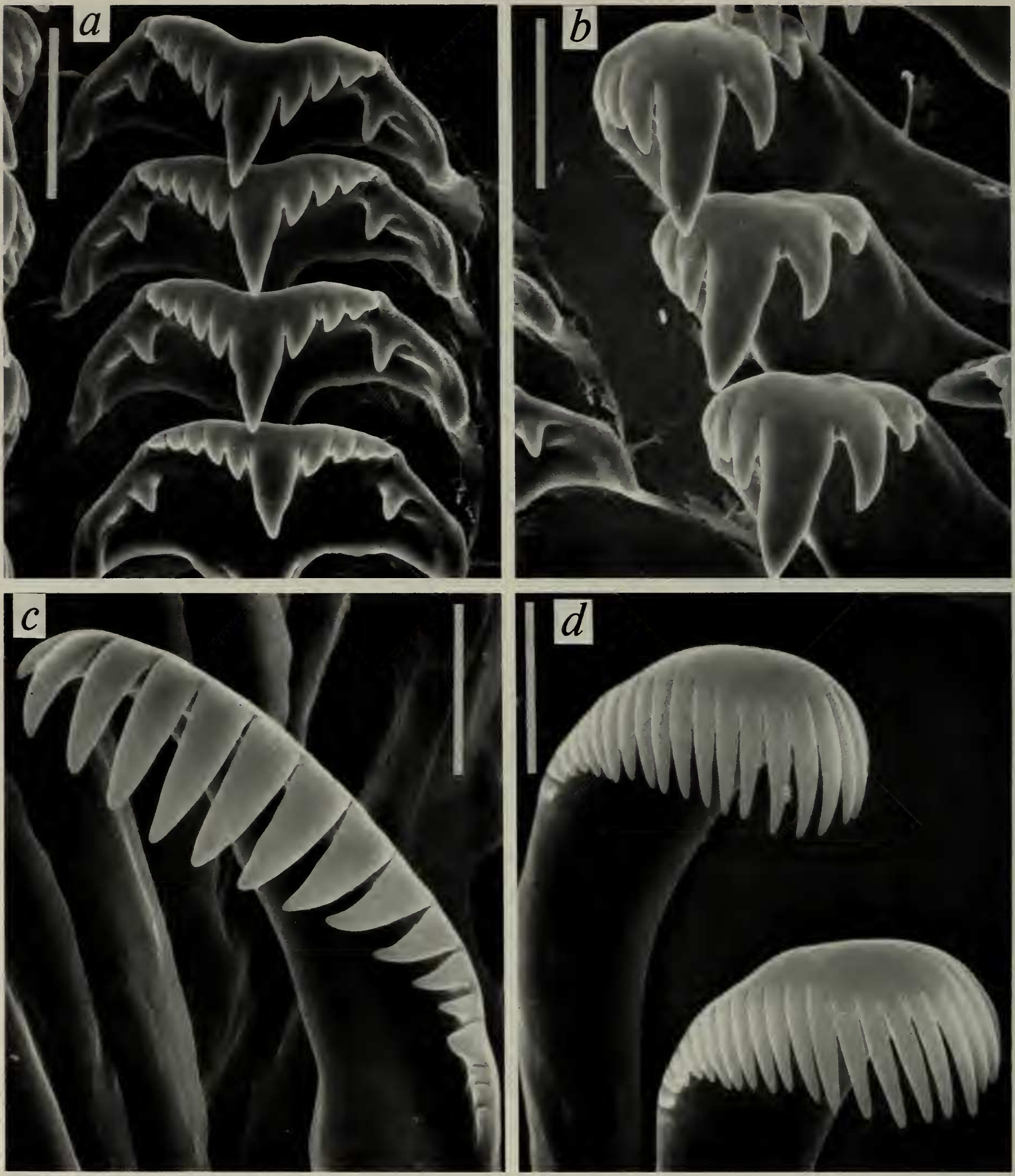

Fig. 60. Radula of *T. rowlandsi,* USNM 857953, Grapevine Springs, upper warm spring: a, Centrals (bar = 15 μm); b, Laterals (bar = 13.6 μm); c, Inner marginal (bar = 6.0 μm); d, Outer marginals (bar = 5.0 μm).

means for potential exchange of aquatic fauna) across current drainage divides imposed by the region's predominant north–south trending basin and range topography. Modern springsnail zoogeography indicates that the above did not facilitate much mixing between pluvial Owens and Amargosa River faunas. These results support earlier con-

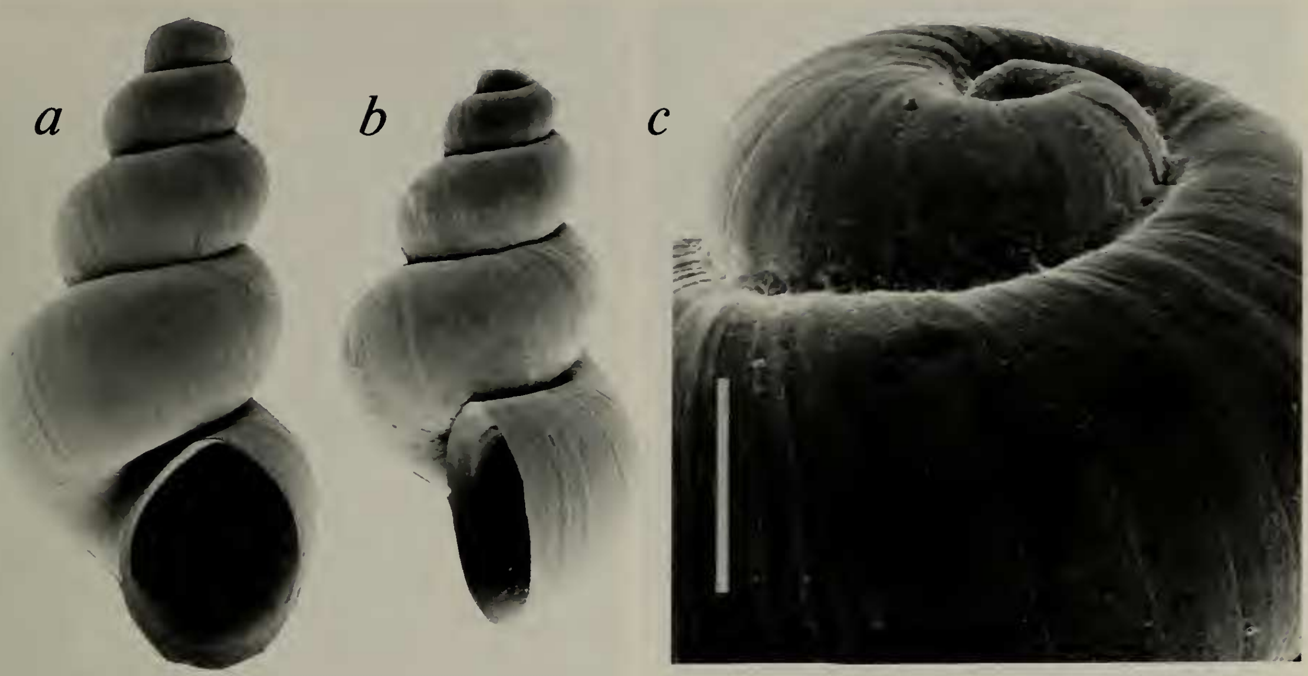

Fig. 61. SEM micrographs of *T. salina* from Cottonball Marsh: a, Holotype, USNM 860410 (3.27 mm); b, c, Paratypes, USNM 853556 (bar = 120 μm).

clusions of Taylor (*in* Miller 1981:58, 1985: 317–318), although his observation that "Spillover from Lake Panamint into Death Valley . . . had no recognizable effect on mollusc distribution" (Taylor 1985:318) is contradicted by distribution of *P. micrococcus* (and possible close affinities between *T. protea* and congeners to the east).

Taylor (1985:317) suggested that faunal exchange between Amargosa and Owens River drainages might have been precluded by a saline dispersal barrier consisting of an arm of Bouse embayment (from former Gulf of California) extending into Death Valley. Although this hypothesis appears plausible, it may not need to be invoked to explain patterns described above. Apart from additional influences on snail distribution imposed by far older lacustrine episodes than considered above (Smith 1984) and other aspects of complex regional geologic/hydrologic history (Minckley et al. 1986), fundamental questions relating to types of habitat occupied by Pleistocene springsnails and plausibility of dispersal of such (frequently stenotopic) organisms along chains of pluvial lakes have not been thoroughly investigated (see Hershler and Minckley 1986). Details such as size, number, and salinity of inter-connected lakes; and length and gradient of lake outlets obviously would affect probability of snail dispersal. Further, other modes of dispersal undoubtedly occurred and could have produced distributions comparable to or conflicting with those predicted by pluvial drainage models. The presence of fauna in isolated basins recently created or devastated by volcanic activity (Long, Adobe Valleys, respectively), or those that either lacked pluvial connections (Saline Valley, Frenchman Flat [Cane Spring]; Hubbs and Miller 1948) or connected with snailless areas (Deep Springs Valley, whose pluvial lake spilled into Eureka Valley; Miller 1928) attests to importance of factors other than late Pleistocene pluvial drainage systems in effecting modern snail distributions in the region. A detailed zoogeographic analysis encompassing the above considerations will be provided following completion of springsnail survey of remaining portions of the Death Valley System.

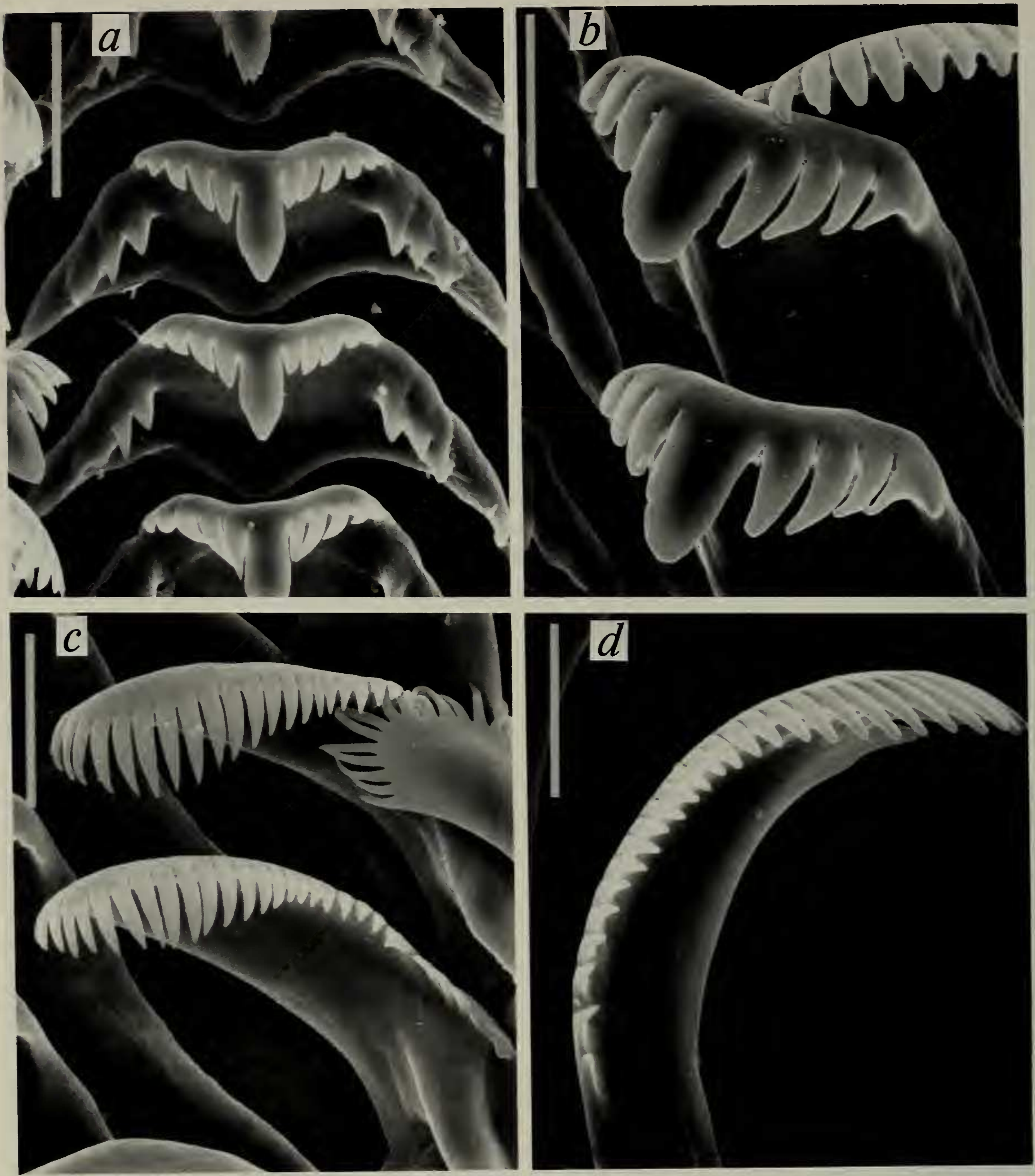

Fig. 62. Radula of *T. salina,* USNM 857998, Cottonball Marsh: a, Centrals (bar = 10 μm); b, Laterals and inner marginal (bar = 7.5 μm); c, Inner and outer marginals (bar = 8.6 μm); d, Outer marginal (bar = 5.0 μm).

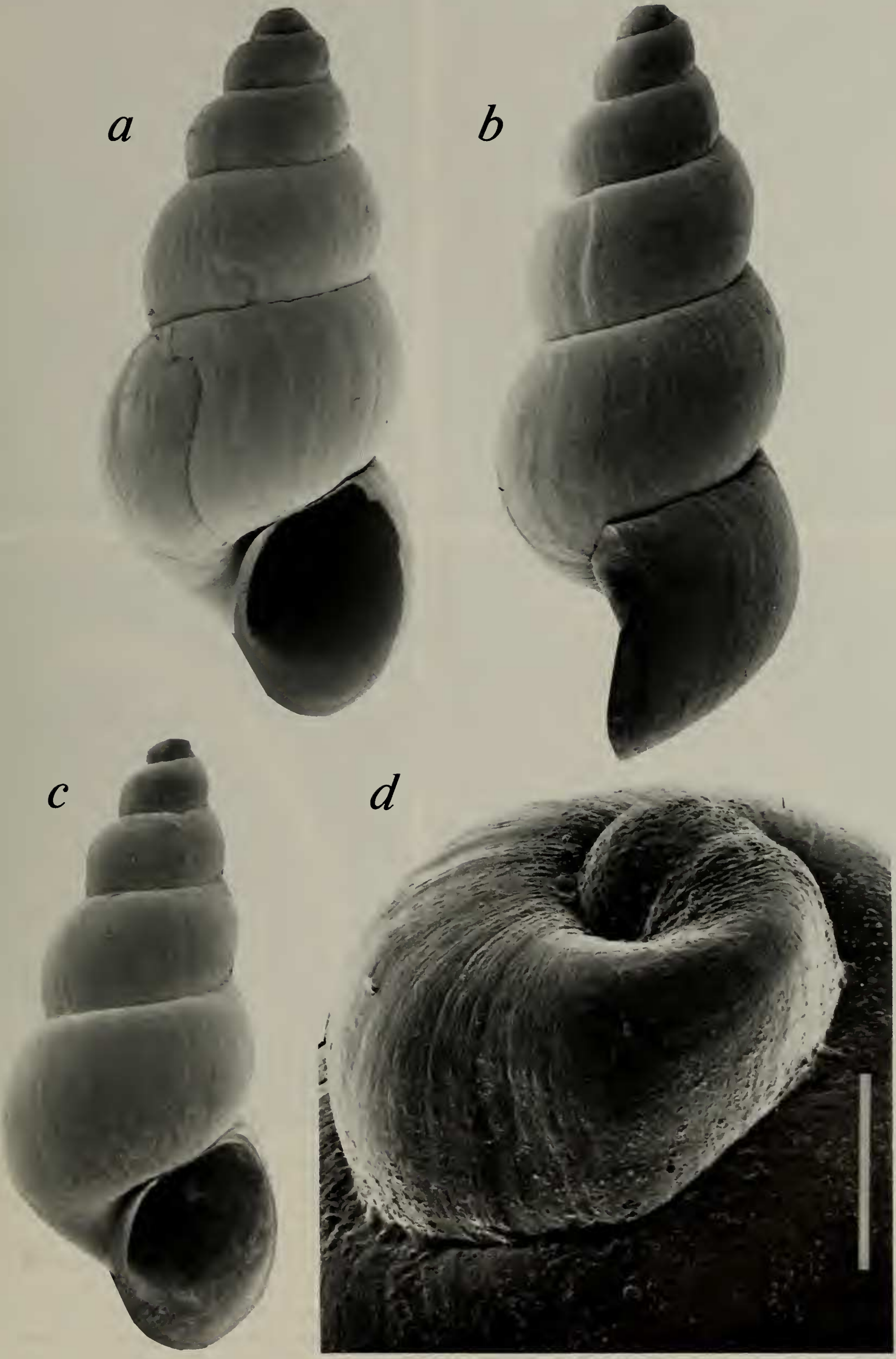

Fig. 63. SEM micrographs of *T. variegata*: a (2.8 mm), b, USNM 853554, Saratoga Spring; c (2.86 mm), d, USNM 853550, Shoshone Spring (bar = 86 μm).

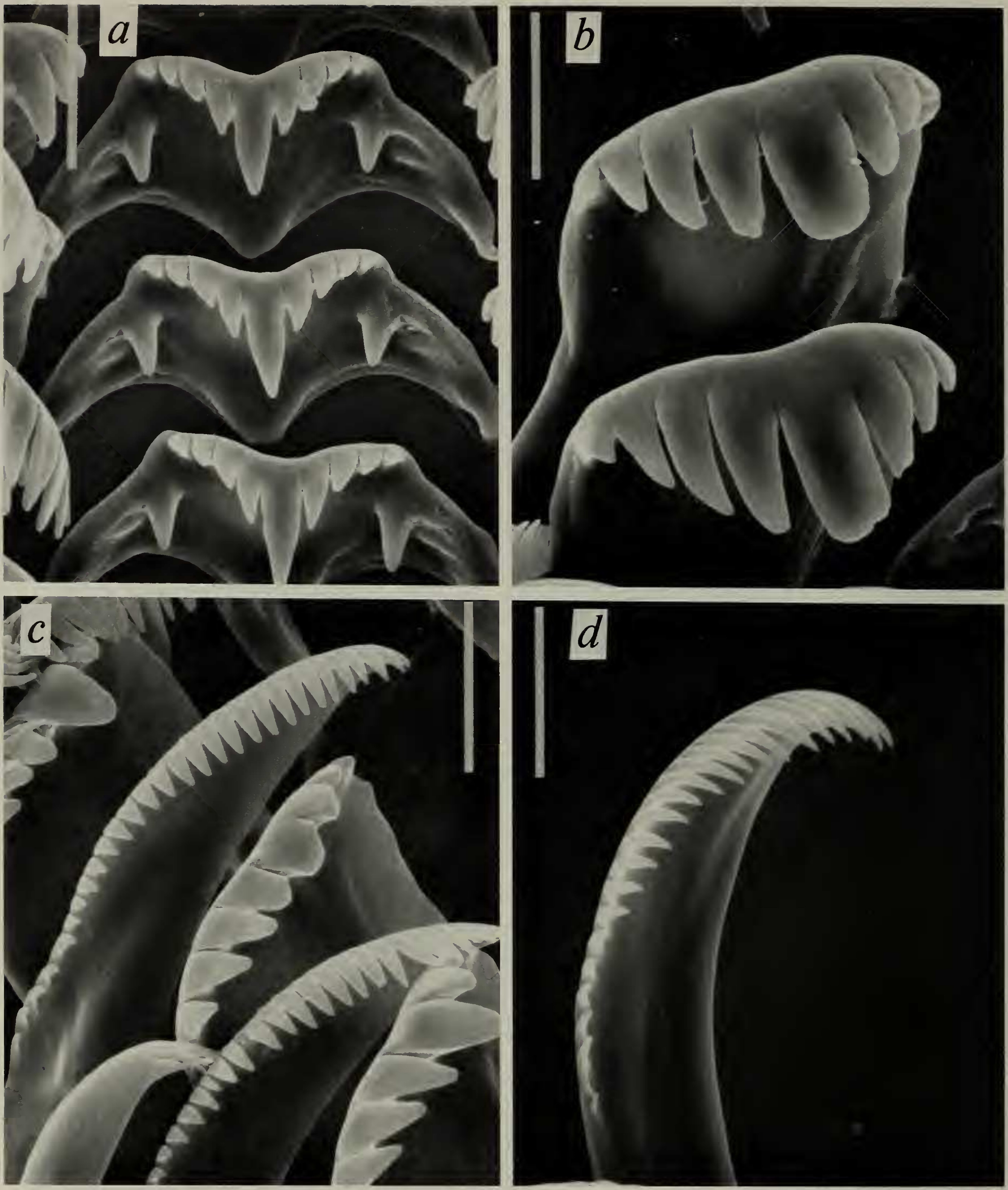

Fig. 64. Radula of *T. variegata*: a, b, USNM 857995, Saratoga Spring (a, centrals, bar = 10.0 μm; b, laterals, bar = 7.5 μm); c, d, USNM 857993, Shoshone Spring (c, laterals and inner marginals, bar = 6.0 μm; d, outer marginal, bar = 4.3 μm).

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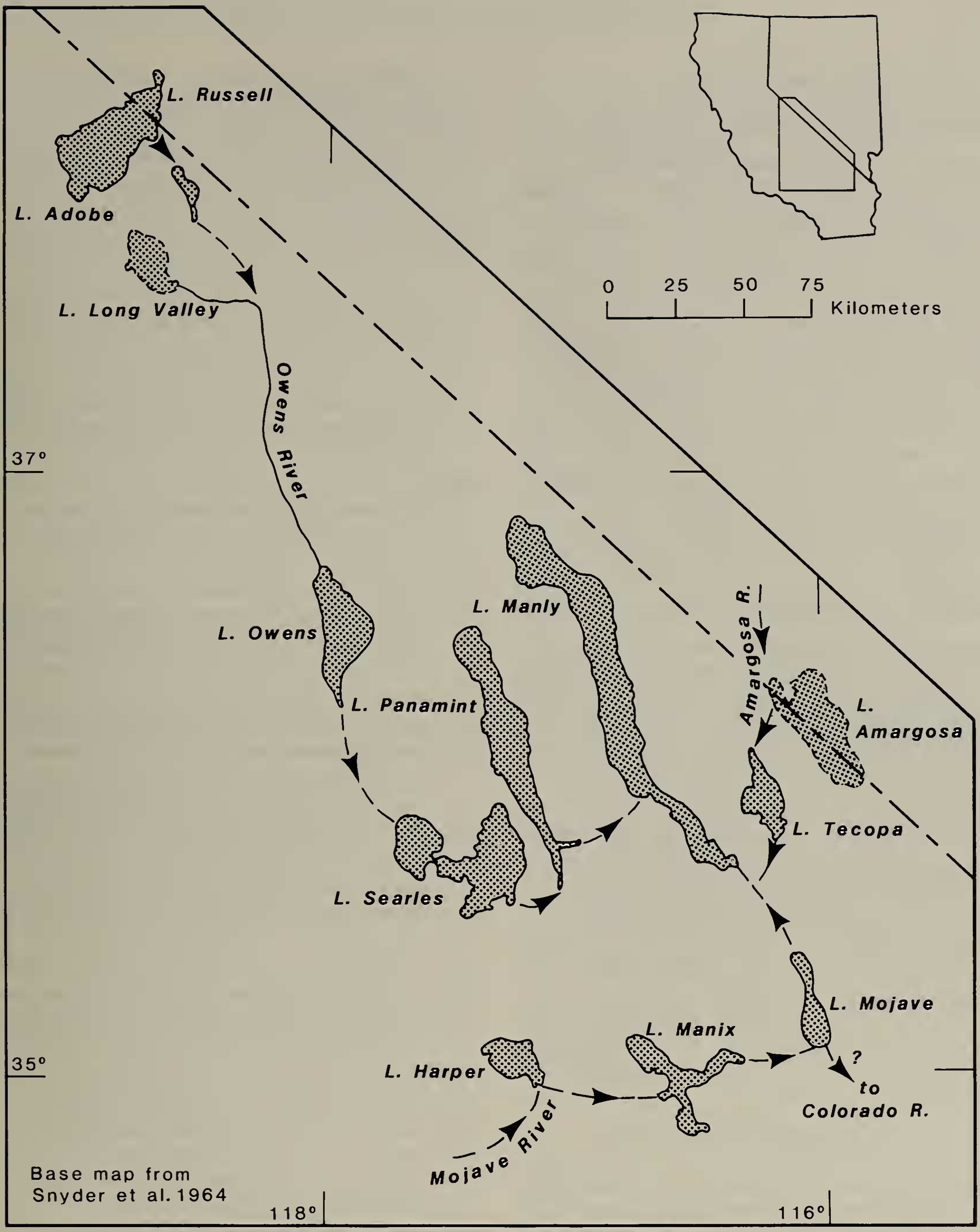
Fig. 65. Map of Pleistocene Death Valley System showing drainage relations (not necessarily contemporaneous). Stippled areas encircled by dashed lines may not have contained lakes for significant portions of the pluvial period. In the northeast, Lake Russell (Mono Valley) spilled into Lake Adobe (Adobe Valley), which in turn overflowed (through a gap in Benton Range) to enter the (now mostly dry) north fork of ancestral Owens River (Putnam 1949; Hubbs and Miller 1948; Gilbert et al. 1968). Lake Long Valley filled shortly after Long Valley caldera was created by explosive eruption of Bishop tuff 700,000 BP (Bailey et al. 1976), and spilled into south fork of Owens River. Outflow from Owens Lake, possibly initiated as a result of increased flow due to



capture of upper San Joaquin River drainage in Long Valley (Huber 1981, Smith et al. 1983), passed between Sierra Nevada and Coso Range to enter and fill China and Searles Lakes. Searles Lake overflowed into Panamint Valley, which held a large lake in its southern portion that spilled into Death Valley during several periods between 120,000 and 20,000 BP (Gale 1914, Hooke 1972, Smith 1976, Hale 1984). To the west, the lush wetland of Ash Meadows (that did not have a large pluvial lake; Mifflin and Wheat 1979, Hay et al. 1986) drained at least intermittently to Amargosa River during Pliocene-Pleistocene. Further downflow the river was ponded in mid- to late-Pleistocene by alluvial fans above Amargosa Gorge to form Lake Teopa (Sheppard and Gude 1968, Starkey and Blackmon 1979), which spilled into southern Death Valley. Mojave River filled a series of three pluvial lakes, with Lake Mojave overflowing toward southern Death Valley during several intervals of late Pleistocene from > 14,500–9000 BP (Ore and Warren 1971). Overflow from Death Valley System to Colorado River during an extreme pluvial period is conjectural, and has often been hypothesized based on distribution of aquatic biota (Miller 1981, Taylor 1986). Hale (1984) described an old (pre-Pleistocene) fluvial channel at Ash Hill near Ludlow, CA, that could be a product of such outflow. The channel is at 594 m elevation, which would require a vast pluvial lake (>300 km long and >650 m maximum depth) extending to northern Death Valley: additional geological evidence is needed to confirm this remarkable possibility.

Acknowledgments

Fieldwork in the Death Valley area was supported by Smithsonian Institution Research Opportunity Fund (ROF), Wildlife Conservation International of the New York Zoological Society, and contracts awarded by U.S. Fish and Wildlife Service, Great Basin Complex (Order No. 14320-0182); Bureau of Land Management, California Desert District (CA-060-CT5); and California Fish and Game (C-1922). Collecting permits were provided by National Park Service (Death Valley National Monument) and State of California, and access to sites on Nevada Test Site, China Lakes Naval Weapons Center, and Fort Irwin is also gratefully acknowledged. Bureau of Land Management (District offices in Ridgecrest and Bishop), California Fish and Game (Bishop office), and National Park Service (Death Valley National Monument) loaned field vehicles and provided other forms of logistic support. Field assistance was provided by numerous individuals, especially J. Aardahl, R. Brown, W. Cassidy, T. Ford, D. Giuliani, D. Herbst, B. Kohfield, P. Rowlands, and D. Wong. Heidi Wolf sorted material and produced excellent SEM micrographs. Paul Greenhall digitized shell material. Molly Ryan drew shells and drafted maps (with assistance from C. Flamer).

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Appendix

Collection localities, numbered as in Figs. 2–7. Data include name of site, state, county, topographic sheet, township and range coordinates, site elevation, and date of visitation (for negative sites only).

1. Stream in Sage Canyon. CA: Kern; Horse Canyon, CA (7.5), 7.0 km SW of NE corner of quadrangle, 1342 m. 2. Boulder Spring. CA: Kern; Horse Canyon, CA, 5.6 km S-SW of NE corner of quadrangle, 1251 m, 3-26-87. 3. Stream in Indian Wells Canyon. CA: Kern; Inyokern, CA, NW ¼ sec. 17, T 26S, R 38E, 1068 m, 3-26-87. 4. Spring in SW corner of Short Canyon. CA: Kern; Inyokern, CA, NW ¼ sec. 5, T 26S, R 38E, 1129 m, 3-26-87. 5. Stream in Grapevine Canyon. CA: Kern; Inyokern, CA, center of sec. 29, T 25S, R 38E, 946 m, 3-26-87. 6. Stream in Sand Canyon. CA: Kern; Little Lake, CA, center of sec. 7, T 25S, R 38E, 1068 m. 7. Stream in Noname Canyon. CA: Kern; Little Lake, CA, 10.0 km NE of SW corner of quadrangle, 976 m, 3-26-87. 8. Stream in Ninemile Canyon. CA: Inyo; Little Lake, CA, 12.2 km NE of SW corner of quadrangle, 976 m, 3-26-87. 9. Spring 0.8 km S of Little Lake, W of HW 395. CA: Inyo; Little Lake, CA, SE ¼ sec. 18, T 23S, R 38E, 946 m, 4-1-87. 10. Spring at Little Lake, E of HW 395. CA: Inyo; Little Lake, CA, NW ¼ sec. 17, T 23S, R 38E, 946 m. 11. Stream in Little Lake Canyon. CA: Inyo; Little Lake, CA, NE ¼ sec. 12, T 23S, R 37E, 1129 m, 4-1-87. 12. Springs ca. 1.0 km N of Little Lake Canyon. CA: Inyo; Little Lake, CA, SW ¼ sec. 1, T 23S, R 37E, 1159 m, 4-30-87. 13. Stream in canyon ca. 3.0 km N of Little Lake Canyon. CA: Inyo; Little Lake, CA, 4.4 km SE of NW corner of quadrangle, 1220 m, 4-30-87. 14. Stream in Portugese Canyon. CA: Inyo; Haiwee Reservoir, CA, 2.19 km NE of SW corner of quadrangle, 1342 m, 4-1-87. 15. Springs on Portugese Bench. CA: Inyo; Haiwee Reservoir, SW corners of secs. 3, 10, T 22S, R 37E, 1160–1220 m, 4-30-87. 16. Lower spring in Tunawee Canyon. CA: Inyo; Haiwee Reservoir, CA, SW ¼ sec. 33, T 21S, R 37E, 1373 m, 4-25-87. 17. Upper spring in Tunawee Canyon. CA: Inyo; Monache Mtn., CA, 7.0 km N-NW of SE corner of quadrangle, 1525 m, 4-30-87. 18. Haiwee Creek. CA: Inyo; Monache Mtn., CA, 12.6 km S-SW of NE corner of quadrangle, 1586 m, 4-30-87. 19. Springs in (2) unnamed canyons N of Haiwee Canyon. CA: Inyo; Monache Mtn., CA, NW corners secs. 30, 31, T 20S, R 37E, 1556 m, 4-30-87. 20. Hogback Creek. CA: Inyo; Monache Mtn., CA, 7.3 km SW of NE corner of quadrangle, 1586 m. 21. Summit Creek. CA: Inyo; Monache Mtn., CA, NE ¼ sec. 7, T 20S, R 37E, 1373 m. 22. Spring ca. 3.0 km N of Summit Creek. CA: Inyo; Monache Mtn, CA, center of sec. 6, T 20S, R 37E, 1281 m. 23. Walker Creek. CA: Inyo; Monache Mtn., CA, NE ¼ sec. 34, T 19S, R 37E, 1769 m, 4-16-87. 24. Cartago Creek. CA: Inyo; Olancha, CA, NE ¼ sec. 11, T 19S, R 37E, 1159 m, 4-16-87. 25. Spring at Cabin Bar Ranch, ca. 2.5 km N of Olancha. CA: Inyo; Olancha, CA, SW ¼ sec. 6, T 19S, R 37E, 1098 m. 26. Braley Creek and springs just to S. CA: Inyo; Olancha, CA, 10.0 km NW of SE corner of quadrangle, 1190 m, 4-16-87. 27. Springs on edge of Owens Lake at Permanente. CA: Inyo; Olancha, CA, 13.8 km N of SE corner of quadrangle, 1068 m, 2-9-85. 28. Ash Creek. CA: Inyo; Olancha, CA, 15.6 km NW of SE corner of quadrangle, 1068 m, 4-16-87. 29. Cottonwood Creek. CA: Inyo; Olancha, CA, 9.6 km SW of NE corner of quadrangle, 1037 m, 4-16-87. 30. Lower Centennial Spring. CA: Inyo; Keeler, CA, 2.3 km W of SE corner of quadrangle, 1769 m, 3-31-87. 31. Dirty Socks (Hot Spring). CA: Inyo; Keeler, CA, NE ¼ sec. 34, T 18S, R 37E, 1098 m, 2-9-85. 32. Springs at S end of Owens Lake, ca. 3.5 km NW of Dirty Socks. CA: Inyo; Keeler, CA, NW ¼ sec. 17, T 18S, R 38E, 1098 m, 2-9-85. 33. Springs on edge of Owens Lake, ca. 3.0 km S of Keeler. CA: Inyo; Keeler, CA, NW ¼ sec. 22, T 17S, R 38E, 1098 m, 4-25-87. 34. Lubkin Creek and spring feeding creek from south. CA: Inyo; Lone Pine, CA, SE ¼ sec. 16, T 16S, R 36E, 1220 m. 35. Spring along E side of Tuttle Creek. CA: Inyo; Lone Pine, CA, NE ¼ sec. 6, T 16S, R 36E, 1281 m. 36. Hogback Creek. CA: Inyo; Lone Pine, CA, NW ¼ sec. 2, T 15S, R 35E, 1159 m. 37. Spring at NE end of Alabama Hills, ca. 4.2 km N-NW of Lone Pine. CA: Inyo; Lone Pine, CA, NE ¼ sec. 31, T 14S, R 36E, 1159 m, 4-25-87. 38. George Creek. CA: Inyo; Lone Pine, CA, NE ¼ sec. 27, T 14S, R 35E, 1251 m, 4-25-87. 39. Independence Creek. CA: Inyo; Independence, CA, SE ¼ sec. 23, T 13S, R 34E, 1342 m, 4-17-87. 40. Boron Springs. CA: Inyo; Mt. Pinchot, CA, NW ¼ sec. 22, T 13S, R 34E, 1556 m. 41. Oak Creek, south fork. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 10, T 13S, R 34E, 1525 m, 4-17-87. 42. Springs ca. 1.0 km W of Mt. Whitney Fish Hatchery. CA: Inyo; Mt. Pinchot, CA, SE ¼ sec. 3, T 13S, R 34E, 1342 m, 4-18-87. 43. Stream in Charlie Canyon. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 3, T 13S, R 34E, 1617 m. 44. Springs feeding N fork Oak Creek. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 3, T 13S, R 34E, 1586 m, 4-25-87. 45. Oak Creek, north fork. CA: Inyo; Mt. Pinchot, CA, center of sec. 3, T 13S, R 34E, 1525 m, 4-17-87. 46. Grover Anton Spring. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 20, T

12S, R 34E, 1586 m, 4-18-87. 47. Harry Birch Springs. CA: Inyo; Mt. Pinchot, CA, NW ¼ sec. 17, T 12S, R 34E, 1464 m, 4-18-87. 48. Sawmill Creek. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 9, T 12S, R 34E, 1251 m, 4-17-87. 49. Division Creek and Scotty Springs just to N. CA: Inyo; Mt. Pinchot, CA, SW ¼ sec. 1, T 12S, R 33E, 1739 m, 4-17-87. 50. Goodale Creek. CA: Inyo; Mt. Pinchot, CA, SE ¼ sec. 17, T 11S, R 34E, 1251 m, 4-18-87. 51. Taboose Creek. CA: Inyo; Big Pine, CA, SE ¼ sec. 8, T 11S, R 34E, 1281 m, 4-18-87. 52. Tinnemaha Creek. CA: Inyo; Big Pine, CA, NW ¼ sec. 28, T 10s, R 34E, 1281 m, 4-18-87. 53. Springs N of Tinnemaha Creek and W of Poverty Hills. CA: Inyo; Big Pine, CA, NE ¼ sec. 30, T 10S, R 34E, 1403 m, 4-18-87. 54. Big Pine Creek. CA: Inyo; Big Pine, CA, SE ¼ sec. 24, T 9S, R 33E, 1373 m, 4-18-87. 55. Baker Creek. CA: Inyo; Big Pine, CA, NE ¼ sec. 13, T 9S, R 33E, 1312 m, 4-18-87. 56. Big Pine Spring. CA: Inyo; Big Pine, CA, NE ¼ sec. 16, T 9S, R 33E, 1891 m, 4-18-87. 57. Spring on hill S of Warren Lake. CA: Inyo; Big Pine, CA NE ¼ sec. 16, T 9S, R 33E, 1220 m. 58. Springs in canyon W of Warren Lake. CA: Inyo; Big Pine, CA, SW ¼ sec. 2, T 9S, R 33E, 1251 m, 4-18-87. 59. Springs in canyon S of Shannon Canyon. CA: Inyo; Big Pine, CA, SW ¼ sec. 33, T 8S, R 33E, 1373 m. 60. Springs N of Klondike Lake. CA: Inyo; Big Pine, CA, SW ¼ sec. 23, T 8S, R 34E, 1208 m, 5-1-87. 61. Freeman Creek. CA: Inyo; Big Pine, CA, NE ¼ sec. 20, T 8S, R 33E, 1434 m, 4-18-87. 62. Spring S of Rawson Creek. CA: Inyo; Bishop, CA, center of sec. 6, T 8S, R 33E, 1434 m, 4-18-87. 63. Spring in Chipmunk Canyon. CA: Inyo; Bishop, CA, SW ¼ sec. 28, T 7S, R 32E, 1708 m, 4-20-87. 64. Stream in Buttermilk Country. CA: Inyo; Mt. Tom, CA, NE ¼ sec. 31, T 7S, R 31E, 2349 m, 5-1-87. 65. Stream in McGee Meadow. CA: Inyo; Mt. Tom, CA, NE ¼ sec. 22, T 7S, R 31E, 1800 m, 4-24-87. 66. Spring in Deep Canyon. Mt. Tom, CA, center of sec. 12, T 7S, R 31E, 1555 m, 4-29-87. 67. Horton Creek. CA: Inyo; Mt. Tom, CA, center of sec. 33, T 6S, R 31E, 1495 m, 4-28-87. 68. Springs N of Horton Creek. CA: Inyo; Mt. Tom, CA, SW ¼ sec. 32, T 6S, R 31E, 1586 m, 4-28-87. 69. Spring along N side of upper Pine Creek. CA: Inyo; Mt. Tom, CA, NE ¼ sec. 26, T 6S, R 30E, 1830 m. 70. Springs entering Pine Creek in Birchim Canyon. CA: Inyo; Mt. Tom, CA, SE ¼ sec. 9, T 6S, R 31E, 1373 m. 71. Spring in Wells Meadow. CA: Inyo; Mt. Tom, CA, NW ¼ sec. 2, T6S, R 31E, 1617 m, 4-24-87. 72. Spring W of Sierra Paradise. CA: Mono; Mt. Tom, CA, NW ¼ sec. 25, T 5S, R 30E, 1769 m, 4-24-87. 73. Stream in Swall Meadow. CA: Mono; Casa Diablo Mtn., CA, NW ¼ sec. 14, T 5S, R 30E, 2196 m, 4-24-87. 74. Spring in Owens Gorge. CA: Inyo; Casa Diablo Mtn., CA, SW ¼ sec. 31, T 4S, R 31E, 1830 m. 75. Fish Slough, "BLM Spring." CA: Mono; Bishop, CA, SW ¼ sec. 30, T 5S, R 33E, 1251 m. 76. Fish Slough, "Northwest Springs." CA: Mono; White Mtn. Peak, CA, SE ¼ sec. 13, T 5S, R 32E, 1281 m. 77. Fish Slough, "NE Spring." CA: Mono; White Mtn. Peak, CA, NW ¼ sec. 18, T 5S, R 33E, 1281 m. 78. Antelope Spring. CA: Mono; Casa Diablo Mtn., CA, SW ¼ sec. 9, T 4S, R 31E, 1830 m, 5-1-87. 79. Moran Spring. CA: Mono; Casa Diablo Mtn., CA, SW ¼ sec. 29, T 3S, R 31E, 2104 m, 5-1-87. 80. Banner Springs. CA: Mono; Casa Diablo Mtn., CA, SE ¼ sec. 18, T 3S, R 31E, 2196 m, 5-1-87. 81. Spring by Tower Mine. CA: Mono; Casa Diablo Mtn., CA, SE ¼ sec. 3, T 3S, R 31E, 1952 m, 4-21-87. 82. Springs entering Marble Creek. CA: Mono; White Mtn. Peak, CA, SE ¼ sec 28, T 2S, R 32E, 1525 m. 83. Marble Creek at HW 6. CA: Mono; White Mtn. Peak, CA, NE ¼ sec. 28, T 2S, R 32E, 1525 m, 4-21-87. 84. Springs ca. 3.0 km S of Benton, W of HW 6. CA: Mono; Benton, NV-CA, SE ¼ sec. 8, T 2S, R 32E, 1617 m, 4-21-87. 85. Benton Hot Springs. CA: Mono; Glass Mountain, CA-NV, SW ¼ sec. 2, T 2S, R 31E, 1708 m, 4-21-87. 86. Springs at N end of Blind Spring Valley. CA: Mono; Glass Mountain, CA-NV, SW ¼ sec. 36, T 1S, R 31E, 1708 m. 87. Springs at Bramlette Ranch. CA: Mono; Benton, NV-CA, SW ¼ sec. 6 (springsnail positive), SE ¼ sec. 6 (negative), T 1S, R 32E, 1678 m, 4-21-87. 88. Stream in Long John Canyon. CA: Inyo; New York Butte, CA, 14.4 km N-NE of SW corner of quadrangle, 1769 m, 5-4-87. 89. French Spring. CA: Inyo, New York Butte, CA, 8.8 km S of NW corner of quadrangle, 1617 m. 90. Spring in Willow Springs Canyon. CA: Inyo; Independence, CA, 6.5 km NW of SE corner of quadrangle, 1861 m, 8-18-87. 91. Barrel Springs. CA: Inyo, Independence, CA, 13.6 km SW of NE corner of quadrangle, 1952 m. 92. Spring ca. 1.6 km SE of Mule Spring. CA: Inyo; Waucoba Mtn., CA, 11.7 km N-NE of SW corner of quadrangle, 1586 m. 93. Mule Spring. CA: Inyo, Waucoba Mtn., CA, SE ¼ sec. 1, T 10S, R 34E, 1312 m. 94. Spring at Graham Ranch. CA: Inyo, Waucoba Mtn., CA, NE ¼ sec. 12, T9S, R 34E, 1373 m. 95. Ulymeyer Spring. CA: Inyo; Waucoba Mtn., CA, NE ¼ sec. 10, T 9S, R 34E, 1235 m, 4-19-87. 96. Wilkerson Springs. CA: Inyo, Waucoba Mtn., CA, NW ¼ sec. 10, T 9S, R 34E, 1220 m. 97. Spring at Toll House. CA: Inyo, Waucoba Mtn., CA, NE ¼ sec. 24, T 8S, R 34E, 1861 m. 98. Warm Springs. CA: Inyo, Bishop, CA, SW ¼ sec. 8, T 8S, R 34E, 1220 m. 99. Spring S of Poleta Canyon. CA: Inyo; Bishop, CA, SE ¼ sec. 18, T 7S, R 34E, 1373 m, 5-4-87. 100. Spring S of Silver Canyon. CA: Inyo; Bishop, CA, SE ¼ sec. 26, T6S, R 33E, 1281 m, 4-26-87. 101. Stream in Silver Canyon. CA: Inyo; Bishop, CA, SE ¼ sec. 24, T 6S, R 33E, 1434 m, 4-26-87. 102. Stream in Coldwater Canyon. CA: Mono; Bishop, CA, SE ¼ sec. 26, T 5S, R 33E, 1494 m, 5-3-87. 103. Springs on bench S of Piute Creek. CA: Mono, Bishop, CA, SE ¼ sec. 22, T 5S, R 33E, 1342 m. 104. Stream in canyon S of Piute Creek. CA: Mono, Bishop, CA, NE ¼ sec. 23, T 5S, R 33E, 1617 m. 105. Spring S of Millner Creek at Copper Queen Mine. CA: Mono; White Mtn. Peak, CA, NE ¼ sec. 21, T 4S, R 33E, 1586 m, 4-28-87. 106. Spring

S of Lone Tree Creek at Hill Ranch. CA: Mono; White Mtn. Peak, CA, NE ¼ sec. 5, T 4S, R 33E, 1617 m, 4-22-87. 107. Birch Creek. CA: Mono; White Mtn. Peak, CA, SE ¼ sec. 7, T 3S, R 33E, 1617 m, 4-22-87. 108. Orchard Spring. NV: Mineral; Benton, NV-CA, SW ¼ sec. 35, T 1N, R 32E, 2135 m, 5-10-87. 109. Spring in Queen Canyon. NV: Mineral; Benton, NV-CA, SE ¼ sec. 25, T 1N, R 32E, 2166 m, 5-10-87. 110. Stream in Queen Canyon (above spring). NV: Mineral; Benton, NV-CA, NE ¼ sec. 36, T 1N, R 32E, 2288 m, 5-10-87. 111. Springs just downslope from Long Valley Dam. CA: Mono; Casa Diablo Mtn., CA, NW ¼ sec. 20, T 4S, R 30E, 1922 m, 5-3-87. 112. Stream on W side of Little Round Valley. CA: Mono; Casa Diablo Mtn., CA, SE ¼ sec. 36, T 4S, R 29E, 2105 m, 4-23-87. 113. McGee Creek. CA: Mono; Mt. Morrison, CA, 7.9 km NW of SE corner of quadrangle, 2501 m, 4-23-87. 114. Stream (W of Convict Creek) feeding Convict Lake. CA: Mono; Mt. Morrison, CA, SW ¼ sec. 22, T 4S, R 28E, 2562 m, 4-27-87. 115. Springs on S side of HW 395 W of Crowley Lake. CA: Mono; Mt. Morrison, CA, SW ¼ secs. 1 (4-23-87) and 2 (4-29-87), T 4S, R 28E, 2172 m. 116. Spring E of Laurel Creek. CA: Mono; Mt. Morrison, CA, NE ¼ sec. 9, T 4S, R 28E, 2196 m, 4-29-87. 117. Whitmore Hot Springs. CA: Mono; Mt. Morrison, CA, NE ¼ sec. 6, T 4S, R 29E, 2105 m, 4-29-87. 118. Springs at Hot Creek Hatchery. CA: Mono; Mt. Morrison, CA, SW ¼ sec. 35, T 3S, R 28E, 2166 m, 4-23-87. 119. Springs at Hot Creek Ranch. CA: Mono; Mt. Morrison, CA, SE ¼ sec. 35, T 3S, R 28E, 2166 m, 4-23-87. 120. Casa Diablo Hot Springs (cool seeps). CA: Mono; Mt. Morrison, CA, NW ¼ sec. 32, T 3S, R 28E, 2257 m, 4-23-87. 121. Hot Creek. CA: Mono, Mt. Morrison, CA, NE ¼ sec. 25, T 3S, R 28E, 2196 m. 122. Layton Springs (unnamed on topographic sheet). CA: Mono, Casa Diablo Mtn., CA, SE ¼ sec. 36, T 3S, R 29E, 2074 m. 123. Springs feeding Little Alkali Lake. CA: Mono; Mt. Morrison, CA, SW ¼ sec. 20, T 2S, R 29E, 2104 m, 4-29-87. 124. Little Hot Creek (source). CA: Mono; Mt. Morrison, CA, NW ¼ sec. 13, T 3S, R 28E, 2074 m, 5-6-87. 125. Deadman Creek. CA: Mono; Mt. Morrison, CA, NE ¼ sec. 27, T2S, R 27E, 2257 m, 4-29-87. 126. Big Springs. CA: Mono; Cowtrack Mtn., CA, NE ¼ sec. 25, T 2S, R 27E, 2166 m, 4-23-87. 127. Spring ca. 0.5 km E-NE of Arcularius Ranch. CA: Mono; Cowtrack Mtn., CA, SE ¼ sec. 20, T 2S, R 28E, 2135 m, 5-6-87. 128. Springs along lower section of McLaughlin Creek. CA: Mono; Cowtrack Mtn., CA, NE ¼ sec. 15, T 2S, R 28E, 2318 m, 5-6-87. 129. McLaughlin Spring. CA: Mono; Cowtrack Mtn., CA, NE ¼ sec. 12, T 2S, R 28E, 2654 m, 5-6-87. 130. Springs at S end of Black Lake. CA: Mono; Glass Mountain, CA-NV, SW ¼ sec. 4, T 2S, R 31E, 1922 m, 4-21-87. 131. Springs at N end of Black Lake. CA: Mono; Glass Mountain, CA-NV, SE ¼ sec. 29, T 1S, R 31E, 1952 m, 4-21-87. 132. River Spring. CA: Mono, Glass Mountain, CA-NV, NE ¼ sec. 24, T 1N, R 30E, 1983 m. 133. Stream in Crooked Meadows. CA: Mono; Cowtrack Mtn., CA, NW ¼ sec. 36, T 1S, R 28E, 2654 m, 5-6-87. 134. Pilot Spring. CA: Mono; Cowtrack Mtn., CA, SE ¼ sec. 27, T 1S, R 28E, 2623 m, 5-6-87. 135. Baxter Spring. CA: Mono; Cowtrack Mtn., CA, SE ¼ sec. 1, T 1S, R 28E, 2623 m, 5-6-87. 136. Gaspipe Spring. CA: Mono; Cowtrack Mtn., CA, NW ¼ sec. 1, T 1S, R 28E, 2440 m, 5-6-87. 137. Indian Spring. CA: Mono; Cowtrack Mtn., CA, 13.4 km SE of NW corner of quadrangle, 2288 m, 5-6-87. 138. Simons Spring (and others in large marshy area). CA: Mono; Cowtrack Mtn., CA, 6.9 km SE of NW corner of quadrangle, 1968 m, 5-5-87. 139. Willow Spring (not shown on topographic sheet). CA: Mono; Cowtrack Mtn., CA, NE ¼ sec. 15, T 1N, R 27E, 1952 m, 5-5-87. 140. Spring along Lee Vining Creek. CA: Mono; Mono Craters, CA, NW ¼ sec. 19, T 1N, R 26E, 2227 m, 5-5-87. 141. Springs feeding lower section of Lee Vining Creek. CA: Mono; Mono Craters, CA, NW ¼ sec. 9, T 1N, R 26E, 2000 m, 5-5-87. 142. Springs along HW 395 ca. 5.0 km NW of Lee Vining. CA: Mono; Mono Craters, CA, NE ¼ sec. 31, T 2N, R 26E, 1950-2075 m, 5-6-87. 143. Lower Dechambeau Creek and associated springs. CA: Mono; Bodie, CA, SE ¼ sec. 19, T 2N, R 26E, 1922 m, 5-6-87. 144. Spring ca. 2.0 km S of Dechambeau Creek along HW 395. CA: Mono; Bodie, CA, SE ¼ sec. 30, T 2N, R 26E, 1922 m, 5-6-87. 145. Mill Creek. CA: Mono; Bodie, CA, NW ¼ sec. 15, T 2N, R 25E, 2379 m, 5-6-87. 146. Stream N of Mill Creek. CA: Mono; Bodie, CA, SE ¼ sec. 1, T 2N, R 25E, 2105 m, 5-6-87. 147. Stream in Rattlesnake Canyon. CA: Mono; Bodie, CA, NW ¼ sec. 30, T 3N, R 26E, 2288 m, 5-6-87. 148. Murphy Spring. CA: Mono; Bodie, CA, SE ¼ sec. 24, T 4N, R 26E, 2501 m, 5-6-87. 149. Stream S of Murphy Spring. CA: Mono; Bodie, CA, NE ¼ sec. 25, T 4N, R 26E, 2410 m, 5-6-87. 150. Stream in Cottonwood Canyon. CA: Mono; Bodie, CA, SE ¼ sec. 32, T 4N, R 27E, 2227 m, 5-6-87. 151. Sulphur Pond and pool to E. CA: Mono; Trench Canyon, CA-NV, SE ¼ sec. 26, T 3N, R 27E, 1952 m, 5-6-87. 152. Saline Marsh. CA: Inyo; New York Butte, CA, center of sec. 27, T 14S, R 28E, 335 m. 153. Stream in Hunter Canyon. CA: Inyo; New York Butte, CA, 14.5 km SE of NW corner of quadrangle, 549 m, 3-28-87. 154. Stream in Beveridge Canyon. CA: Inyo; New York Butte, CA, 12.3 km E-SE of NW corner of quadrangle, 580 m, 3-28-87. 155. Badwater Spring. CA: Inyo; Waucoba Wash, CA, 10.0 km NE of SW corner of quadrangle, 488 m, 3-28-87. 156. Springs S of Lower Warm Springs. CA: Inyo; Waucoba Wash, CA, NE ¼ sec. 30, T 13S, R 39E, 381 m, 3-29-87. 157. Springs NW of Upper Warm Springs. CA: Inyo; Waucoba Wash, CA, SE ¼ sec. 5, T 13S, R 39E, 549 m, 3-29-87. 158. Upper Warm Spring. CA: Inyo; Dry Mountain, CA, NE ¼ sec. 9, T 13S, R 39E, 488 m, 2-11-85. 159. Willow Creek. CA: Inyo; Waucoba Wash, CA, 12.3 km N-NE of SW corner of quadrangle, 915 m, 3-28-87. 160. Corral Springs. CA: Inyo; Blanco

Mtn., CA, SW ¼ sec. 3, T 8S, R 36E, 1525 m. 161. Bog Mounds Springs. CA: Inyo; Blanco Mtn., CA, SW ¼ sec. 32, T 7S, R 36E, 1508 m, 4-26-87. 162. Antelope Spring. CA: Inyo; Blanco Mountain, CA, NW ¼ sec. 24, T 7S, R 35E, 1708 m. 163. Samms Spring. CA: Inyo; Blanco Mountain, CA, SW ¼ sec. 13, T 7S, R 35E, 1739 m, 3-29-87. 164. Willow Spring. CA: Inyo; Magruder Mtn., NV-CA, 10.0 km N-NE of SW corner of quadrangle, 1739 m, 3-30-87. 165. Wheelbarrow Spring (not shown on topographic sheet). CA: Inyo; Soldier Pass, CA-NV, NE ¼ sec. 5, T 7S, R 37E, 1708 m, 3-30-87. 166. Wyman Creek. CA: Inyo; Soldier Pass, CA-NV, SW ¼ sec. 23, T 6S, R 36E, 1769 m, 3-29-87. 167. Stream in Indian Joe Canyon. CA: Inyo; Trona, CA, NW ¼ sec. 24, T 24S, R 42E, 732 m, 4-13-87. 168. Allen Spring (not shown on topographic sheet). CA: Inyo; Trona, CA, NE ¼ sec. 24, T 24S, R 42E, 854 m, 4-13-87. 169. Stream in Great Falls Basin. CA: Inyo; Trona, CA, SW ¼ sec. 12, T 24S, R 42E, 854 m, 4-13-87. 170. Stream in Canyon N of Great Falls Basin. CA: Inyo; Trona, CA, NW ¼ sec 7, T 24S, R 43E, 915 m, 3-25-87. 171. Stream in S fork Homewood Canyon. CA: Inyo; Trona, CA, NW ¼ sec 2, T 24S, R 42E, 1159 m, 3-25-87. 172. Benko Spring. CA: Inyo; Trona, CA, NE ¼ sec. 34, T 23S, R 42E, 1037 m, 3-25-87. 173. Stream in N fork Homewood Canyon. CA: Inyo; Trona, CA, SW ¼ sec. 25, T 23S, R 42E, 1098 m, 3-25-87. 174. Bircham Springs. CA: Inyo; Trona, CA, NE ¼ sec. 20, T 23S, R 42E, 1708 m, 3-4-85. 175. Wild Rose Spring. CA: Inyo; Mountain Springs Canyon, CA, SW ¼ sec. 11, T 23S, R 41E, 1525 m, 3-4-85. 176. LaMotte Spring. CA: Inyo; Trona, CA, NE ¼ sec. 31, T 22S, R 42E, 1525 m, 3-4-85. 177. Stream in N fork Water Canyon. CA: Inyo; Trona, CA, NE ¼ sec. 36, T 22S, R 42E, 1098 m, 4-11-87. 178. Tennessee Spring. CA: Inyo; Coso Peak, CA, SW ¼ sec. 13, T 21S, R 41E, 1830 m. 179. Haiwee Spring. CA: Inyo; Haiwee Reservoir, CA, SW ¼ sec. 10, T 21S, R 39E, 1403 m, 3-5-85. 180. Stream in Knight Canyon. CA: Inyo; Maturango Peak, CA, SE ¼ sec. 14, T 21S, R 42E, 1037 m. 181. Stream in Revenue Canyon. CA: Inyo; Maturango Peak, CA, NW ¼ sec. 3, T 21S, R 42E, 976 m, 4-14-87. 182. Stream in Snow Canyon. CA: Inyo; Maturango Peak, CA, 5.1 km S-SE of NW corner of quadrangle, 1342 m. 183. Black Spring. CA: Inyo; Coso Peak, CA, 1.6 km E of NW corner of quadrangle, 1769 m, 3-31-87. 184. Darwin Wash. CA: Inyo; Darwin, CA, China Garden Spring, NE ¼ sec. 4, T 19S, R 41E, 1037 m; spring above Darwin Falls, NW ¼ sec. 3, T 19S, R 41E, 854 m; stream below falls, SW ¼ sec. 34, T 18S, R 41E, 732 m. 185. Stream in Grapevine Canyon. CA: Inyo; Ubehebe Peak, CA, 8.4 km NW of SE corner of quadrangle, 1525 m, 3-28-87. 186. Big Dodd Spring. CA: Inyo; Ubehebe Peak, CA, 11.5 km NW of SE corner of quadrangle, 1159 m, 3-12-87. 187. Stream in Goler Canyon. CA: Inyo; Manley Peak, CA, 15.3 km NE of SW corner of quadrangle, 549 m, 3-31-87. 188. Anvil Spring. CA: Inyo; Manley Peak, CA, 11.3 km SW of NE corner of quadrangle, 1373 m, 2-18-85. 189. Seepage on SW side of Panamint Lake bed. CA: Inyo; Manley Peak, CA, E sides of secs. 28 and 34, T 22S, R 44E, 317 m, 3-31-87. 190. Stream in Pleasant Canyon. CA: Inyo; Telescope Peak, CA, 6.9 km NE of SW corner of quadrangle, 793 m. 191. Post Office Spring. CA: Inyo; Telescope Peak, CA, NE ¼ sec. 9, T 22S, R 44E, 317 m, 2-14-85. 192. Stream in Happy Canyon. CA: Inyo; Telescope Peak, CA, 11.3 km NE of SW corner of quadrangle, 1098 m, 4-11-87. 193. Spring mounds on Panamint Lake bed NW of Ballarat. CA: Inyo; Maturango Peak, CA, NW ¼ sec. 20, T 21S, R 44E, 323 m, 4-14-87. 194. Stream in Surprise Canyon. CA: Inyo; Telescope Peak, CA, 15.3 km NE of SW corner of quadrangle, 1098 m. 195. Warm Sulphur Springs. CA: Inyo; Telescope Peak, CA, SE ¼ sec. 10, T 21S, R 44E, 305 m, 2-13-85. 196. Stream in Jail Canyon. CA: Inyo; Telescope Peak, CA, 10.0 km SE of NW corner of quadrangle, 1220 m. 197. Stream in Tuber Canyon. CA: Inyo; Telescope Peak, CA, 5.6 km SE of NW corner of quadrangle, 1098 m, 4-11-87. 198. Wildrose Spring. CA: Inyo; Emigrant Canyon, CA, 3.8 km NE of SW corner of quadrangle, 1080 m, 2-15-85. 199. Springs in upper Wildrose Canyon. CA: Inyo; Emigrant Canyon, CA, 5.3 km NE of SW corner of quadrangle, 1220 m, 2-15-85. 200. Cave Spring. CA: San Bernardino; Avawatz Pass, CA, 7.7 km NE of SW corner of quadrangle, 1129 m, 4-9-87. 201. Sheep Creek Spring. CA: San Bernardino; Avawatz Pass, CA, 3.8 km NW of SE corner of quadrangle, 427 m, 4-10-87. 202. Salt Creek E of HW 127. CA: San Bernardino; Avawatz Pass, CA, 14.1 km S-SW of NE corner of quadrangle, 92 m, 3-15-87. 203. Owl Hole Springs. CA: San Bernardino; Leach Lake, CA, NW ¼ sec. 22, T 19N, R 3E, 641 m, 3-16-85. 204. Saratoga Spring. CA: San Bernardino; Avawatz Pass, CA, NW ¼ sec. 2, T 18N, R 5E, 61 m. 205. Ibex Spring. CA: San Bernardino; Shoshone, CA, 8.5 km E-NE of SW corner of quadrangle, 366 m, 3-22-87. 206. Horse Thief Springs. CA: San Bernardino; Horse Thief Springs, CA-NV, 10.4 km E-NE of SW corner of quadrangle, 1403 m, 4-10-87. 207. Willow Spring. CA: Inyo; Tecopa, CA, SW ¼ sec. 25, T 20N, R 7E, 427 m, 3-22-87. 208. Springs in Amargosa Gorge, S of Tecopa. CA: Inyo; Tecopa, CA, NW ¼ sec. 15, T 20N, R 7E, 397 m. 209. Spring in marsh E of Grimshaw Lake. CA: Inyo; Tecopa, CA, NE ¼ sec. 9, T 20N, R 7E, 427 m. 210. Northernmost of Tecopa Hot Springs. CA: Inyo; Tecopa, CA, NW ¼ sec. 33, T 21N, R 7E, 397 m. 211. Shoshone Spring. CA: Inyo; Shoshone, CA, NW ¼ sec. 30, T 22 N, R 7E, 519 m. 212. Resting Spring. CA: Inyo; Tecopa, CA, SE ¼ sec. 31, T 21N, R 8E, 549 m. 213. Lost Spring (unnamed on quadrangle). CA: Inyo; Wingate Wash, CA, 12.8 km SE of NW corner of quadrangle, 702 m, 3-10-87. 214. Salsberry Spring. CA: Inyo; Shoshone, CA, 10.6 km SW of NE corner of quadrangle, 366 m, 3-14-85. 215. Warm Spring. CA: Inyo; Wingate Wash, CA, 7.2 km SE of NW corner of quadrangle, 732 m, 2-18-85. 216. Lower Talc Mine Spring. CA: Inyo; Bennetts Well, CA, 6.4 km E-NE of SW corner of quadrangle, 915 m, 3-10-87. 217. Willow Spring. CA: Inyo; Funeral Peak, CA, 7.8 km NE of SW corner of quadrangle, 732 m, 3-20-87. 218. Hidden Spring. CA: Inyo; Funeral Peak, CA, 15.3 km NE of SW corner of quadrangle, 1342 m, 3-17-87. 219. Springs at Mormon Point. CA: Inyo; Bennetts Well, CA, 6.7 km N-NW of SE corner of quadrangle, −64 m, 3-9-85. 220. Spring (lower) in Johnson Canyon. CA: Inyo; Telescope Peak, CA, SW ¼ sec. 22, T 21S, R 46E, 1190 m. 221. Eagle Borax Spring. CA: Inyo; Bennetts Well, CA, 13.3 km SE of NW corner of quadrangle, −79 m, 2-16-85. 222. Hanaupah Spring. CA: Inyo; Telescope Peak, CA, 7.6 km S-SW of NE corner of quadrangle, 1281 m. 223. Badwater Spring. CA: Inyo; Bennetts Well, CA, 2.7 km SW on NE corner of quadrangle, −79 m, 2-16-85. 224. Tule Spring. CA: Inyo; Bennetts Well, CA, 10.8 km E-SE of NW corner of quadrangle, −79 m, 2-28-85. 225. Grapevine Springs. NV: Nye; Ash Meadows, NV-CA, NE ¼ sec. 2, T 19S, R 50E, 732 m, 3-14-85. 226. Blackwater Spring. CA: Inyo; Emigrant Canyon, CA, 12.9 km S-SW of NE corner of quadrangle, 946 m, 3-10-87. 227. Navel Spring. CA: Inyo; Ryan, CA-NV, NW ¼ sec. 13, T 26N, R 2E, 640 m, 3-17-87. 228. Travertine Springs. CA: Inyo; Furnace Creek, CA, NW ¼ sec. 25, T 27N, R 1E, 122 m. 229. Salt Springs, NW of Cow Creek. CA: Inyo; Chloride Cliff, CA-NV, SW ¼ sec. 21, T 28N, R 1E, −79 m, 2-3-85. 230. Nevares Springs. CA: Inyo; Chloride Cliff, CA-NV, NE ¼ sec. 36, T 28N, R 1E, 275 m. 231. Cottonball Marsh. CA: Inyo; Chloride Cliff, CA-NV, 2.8 km NE of SW corner of quadrangle, −79 m. 232. Salt Springs, W of Cottonball Marsh. CA: Inyo; Chloride Cliff, CA-NV, 1.0 km NE of SW corner of quadrangle, −73 m, 2-22-85. 233. Salt Springs S of Cow Creek. CA: Inyo; Furnace Creek, CA, SE ¼ sec. 3, T 27N, R 1E, 31 m, 2-5-85. 234. Stream in Cottonwood Canyon. CA: Inyo; Marble Canyon, CA, stream 10.0 km NW of SE corner of quadrangle, 732 m, 2-15-85, stream 11.2 km E-NE of SW corner of quadrangle, 1037 m, 3-12-87. 235. McLean Spring (Salt Creek). CA: Inyo; Stovepipe Wells, CA, SW ¼ sec. 31, T 15S, R 46E, 37 m, 3-8-85. 236. Springs NW of Keane Wonder Mine. CA: Inyo; Chloride Cliff, CA-NV, SE ¼ sec. 1, T 15S, R 46E, 366 m, 2-13-85. 237. Monarch Spring. CA: Inyo; Chloride Cliff, CA-NV, SE ¼ sec. 24, T 14S, R 46E, 915 m, 2-4-85. 238. Keane Spring. CA: Inyo; Chloride Cliff, CA-NV, NW ¼ sec. 8, T 30W, R 1E, 1159 m, 2-4-85. 239. Cane Spring. NV: Nye; Cane Spring, NV, 6.0 km N-NE of SW corner of quadrangle, 1238 m. 240. Spring in Oasis Valley, 13.2 km N of Beatty. NV: Nye County; Thirsty Canyon, NV, SE ¼ sec. 32, T 10S, R 47E, 1128 m. 241. Grapevine Springs. CA: Inyo; Ubehebe Crater, CA-NV, NE ¼ sec. 3, T 11S, R 42E, 824 m. 242. Spring 1.6 km E of Scotty's Castle. CA: Inyo; Ubehebe Crater, CA-NV, NW ¼ sec 5, T 11S, R 42E, 946 m. 243. Little Sand Spring. CA: Inyo; Last Chance Range, CA-NV, SE ¼ sec. 17, T 9S, R 41E, 915 m, 387. 244. Sand Spring. CA: Inyo; Last Chance Range, CA-NV, SE ¼ sec. 7, T 9S, R 41E, 946 m, 3-30-87. 245. Last Chance Spring. CA: Inyo; Magruder Mtn., NV-CA, SE ¼ sec. 2, T 8S, R 39E, 1739 m, 3-30-87.